VOLUME 136 PART 2 MARCH 1961

PROCEEDINGS

OF

THE ZOOLOGICAL SOCIETY OF LONDON

LONDON
PUBLISHED BY THE SOCIETY
SOLD AT ITS HOUSE IN REGENT'S PARK, LONDON, N.W.1

Price Thirty Shillings

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THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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Clerk of Publications . . . G. B. STRATTON, M.B.E.

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THE MORPHOLOGY AND FUNCTIONING OF THE MOUTHPARTS OF *CHLOEON DIPTERUM* L. AND *BAETIS RHODANI* PICTET (INSECTA, EPHEMEROPTERA)*

BY

D. SEYMOUR BROWN†

Zoology Department, University of Leicester

[Communicated by Professor H. P. Moon—Accepted 10th May, 1960]

(With 8 figures in the text)

The morphology of the mouthparts of *Chloeon dipterum* L. and *Baetis rhodani* Pictet is described and the manner of functioning of the mouthparts is interpreted on the basis of their morphology and direct observations of feeding larvae. In *C. dipterum* the way in which the mouthparts were used depended upon the nature of the food material. The ways in which the mouthparts of *B. rhodani* differ from those of *C. dipterum* are shown to be consistent with the overall adaptation of the former species to flowing water.

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INTRODUCTION

Many descriptions of the anatomy of larval Ephemeroptera contain accounts of the mouthparts (Lestage 1921, Murphy 1922, Schoenemund 1930, Uéno 1954), and although these are frequently incomplete and the identity of the species described is rarely known with certainty it is clear that there is a great diversity in the external morphology of the mouthparts within the Order. This diversity extends to the intrageneric level and Macan (1950) has demonstrated the value of detailed study of the mouthparts for taxonomic purposes.

The existing accounts of the musculature of the mouthparts (Murphy *loc. cit.*, Strenger 1953) show that intergeneric differences exist, and the disagreement between the accounts by these two authors of the anatomy of *Ecdyonurus*

* Part of a thesis accepted for the degree of Doctor of Philosophy in the University of London.

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suggests the presence of specific characteristics in the internal as well as the external morphology of the mouthparts.

It is likely that these characters form an important part of the adaptation whereby a species is enabled to occupy its particle niche in the aquatic macrohabitat. Hitherto the ecological adaptation of mayfly larvae has been considered almost exclusively in terms of general body shape and the structure of the limbs, and the effect of specialisation in these characters on the feeding mechanism has been neglected. For an understanding of the adaptive radiation of the feeding mechanism in ephemeropteran larvae detailed studies of the food and feeding mechanism in a large number of species are necessary.

The results are given below of a study of the pond-dwelling species *Chloeon dipterum* L., and *Baetis rhodani* Pictet which occurs abundantly in rapidly flowing streams. Both species belong to the "freeswimming" group of ephemeropteran larvae in contrast to the extremely flattened forms *Ecdyonurus* sp. and *Rhithrogena* sp. described by Strenger (*loc. cit.*). In addition *Chloeon* and *Baetis* were of interest in providing an opportunity for determining the ways in which a similar feeding apparatus was adapted to function successfully in habitats as different as a pond and a rapidly flowing stream.

Both Murphy, Strenger, and Dunn (1954) attempted to deduce the way in which the mouthparts functioned from their morphology alone. That this may be a misleading approach is shown by the erroneous conclusion arrived at by early workers (Pictet, 1943, Lampert 1899), from a study of morphology alone, that the diet of ephemeropteran larvae was of a carnivorous nature. Morgan (1913) investigated the feeding mechanism of *Iron fragilis* by direct observation of living animals as well as by dissection, and the same method was used in the case of *C. dipterum* and *B. rhodani* which, being hypognathous, can be observed more successfully than a flattened form such as *Iron*.

MATERIALS AND METHODS

The external morphology of the mouthparts was investigated in whole animals and ecdysed skins, permanent preparations being mounted upon large cover slips so that they could be examined under high magnification from both sides. Musculature was studied by dissection of the heads of specimens fixed in Bouin's fluid (alcoholic).

Observation of larvae was carried out in small aquaria and plane sided jars, furnished with material gathered from the natural habitat, by means of a binocular microscope on a travelling arm. The relatively low magnification necessary allowed a wide depth of focus that enabled the larvae to be followed fairly easily in the large containers. In the case of *B. rhodani*, the natural conditions of the habitat were simulated as far as possible by causing the water to circulate over the substratum by blowing compressed air through one end of the container.

In the anatomical descriptions the terms posterior and anterior are used in relation to the posterior and anterior poles of the longitudinal axis of the animal, i.e., the surfaces on the caudal side of an appendage are referred to as posterior. When muscles are described in the text they are accompanied by the numbers with which they are labelled in the figures.

THE MORPHOLOGY OF THE MOUTHPARTS OF *C. DIPTERUM*

Understanding of the spatial relationships of the mouthparts is aided by a preliminary knowledge of the structure of the head capsule to which the mouthparts are attached.

The head capsule

The external features of the head capsule are reminiscent of those of an orthopteriod insect such as *Periplaneta* or *Locusta*. The long axis of the head is held approximately vertically; there is a demarcation into an anterior surface, composed of vertex, frons and genae (Fig. 1a), and a posterior surface composed of vertex, occiput, postocciput, and post genae (Fig. 1b). The coronal suture extends from its point of junction with the postoccipital suture in the rim surrounding the occipital foramen (Fig. 1b) to a point just above the lateral ocelli where it divides into two frontal sutures extending below the lateral ocelli (Fig. 1a). The compound eyes occupy the dorsal corners of the anterior surface of the head capsule, and the median ocellus is situated midway between the top of the vertex and the epistomal suture (Fig. 1a).

It has not been possible to make out ocular and subocular sutures corresponding to those described in *Locusta* by Albrecht (1953), and the posterior sclerites of the head capsule are indistinguishably fused together in *C. dipterum* as is the case in the species of *Ecdyonurus* described by Strenger (1953). The terms post genae and vertex are used to designate parts of the posterior wall of the head capsule in a way that corresponds as closely as possible to the usage of Strenger.

A large part of the posterior wall of the head capsule is pierced by the occipital foramen through which pass the oesophagus and the neck muscles. These muscles are inserted on the thick ridge which forms the dorsal and lateral boundaries of the occipital foramen and which contains the post occipital suture between the occiput and the postocciput. The postocciput is for the most part a delicate membrane that is easily lost in detaching the head from the body. Ventrally and externally the occipital foramen is bounded by the base of the postmentum, while internally the median edges of the post genae are connected by the body of the hypopharynx (Figs. 1b, 1c & 2a). Between the hypopharynx body and the postmentum lies the sub-oesophageal ganglion of the central nervous system.

The tentorium body projects forward from its ventral edge into the head and divides into paired dorsal and anterior tentorial arms (Figs 1c & 2a). A pair of very small posterior arms project backwards from the tentorium body and fuse with the postocciput forming the postoccipital condyles (Fig. 1b). The dorsal tentorial arms are slender and pass antero-dorsally fusing with the vertex dorso-lateral to the insertion of the antennae (Figs. 1a & 2b). Far more strongly developed are the anterior arms which provide places of origin for several large muscles (Fig. 1c), and serve to brace the ventral margin of the head capsule against the stresses developed during the movements of the mouthparts. They pass antero-ventrally as broad bars fusing with the inflected genae dorsal to the ventral edge of the head capsule (Figs. 1c & 2a). As is the case in *Ecdyonurus* there is no definite boundary between the anterior

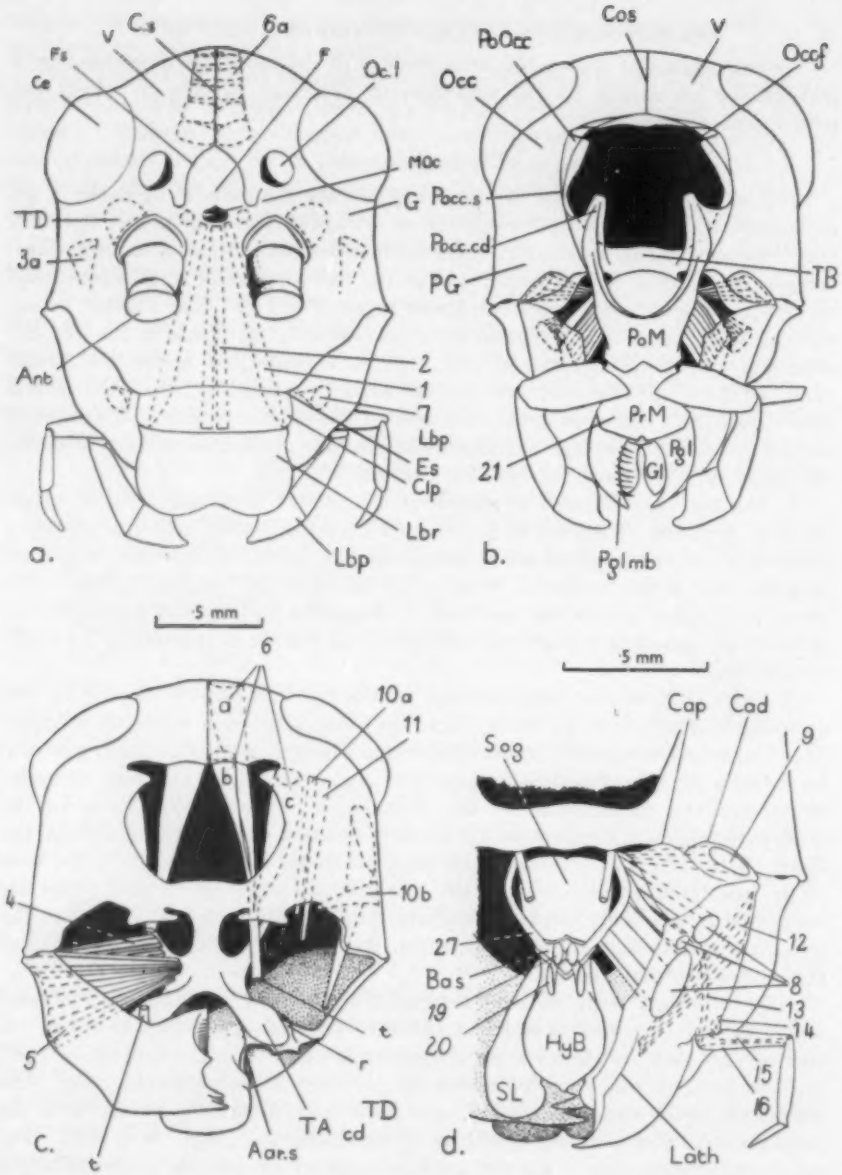

Fig. 1.—*Chloeon dipterum*

a. Head capsule. Anterior surface, showing origins of muscles ; b. Head capsule. Posterior surface, oesophagus and cervical muscles removed ; c. Head capsule. Posterior view, mouthparts removed with the exception of the left mandible ; d. Head capsule. Posterior view of ventral part, labium removed showing the posterior surfaces of the hypopharynx and the right maxilla. (Key to lettering p. 175.)

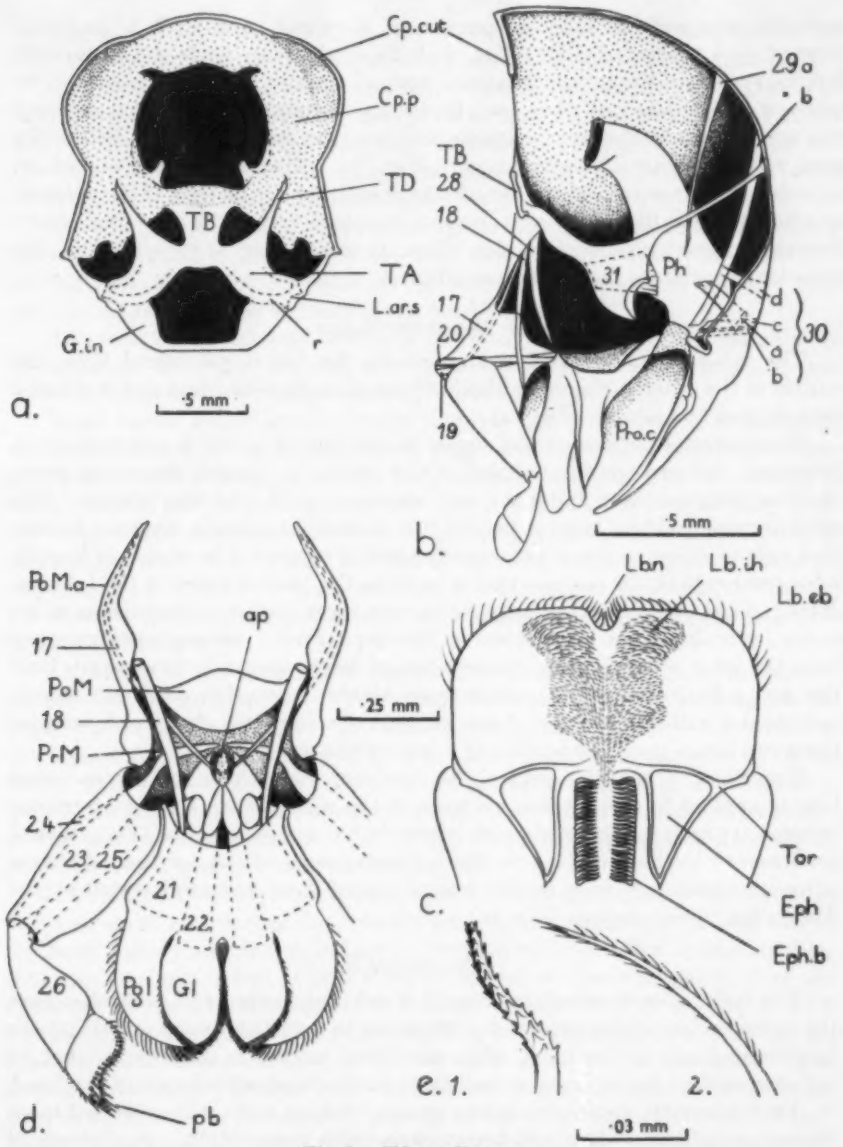

Fig. 2.—*Chloeon dipterum*

a. Tentorium displayed by cutting away the anterior surface of the head capsule ; b. Head capsule viewed laterally with the near lateral and posterior wall removed together with the mandibles and maxillae, to show the preoral cavity and pharynx, and the relationship between the labium and the hypopharynx. The anterior arm of the tentorium is cut through just beyond the base of the dorsal arm ; c. Clypeo-labral lobe, posterior surface ; d. Labium, anterior surface ; e. (i) bristle from notch of labrum ; (ii) bristle from lateral edge of labrum. (Key to lettering p. 175.)

tentorial arm and the inflected margin of the head capsule; it is probably marked by a thickened ridge (Figs. 1c & 2a, r) that surrounds the posteriorly bulging surface of the anterior tentorial arm. Laterally the ridge bears a narrow grooved projection (cd), that contributes to the lateral articulation between the mandible and the head capsule and may be seen projecting below the gena when the head is viewed laterally (Fig. 7b). The ventral inflection of the capsule edge extends from the anterior tentorial arm to the base of the clypeus, at which point it fuses with an inflection from each end of the epistomal suture forming a heavily sclerotised slot (Figs. 1c & 3a, A.ar s) that receives the anterior articulatory facet of the mandible.

The clypeo-labral lobe

The mouthparts are enclosed anteriorly by the clypeo-labral lobe, the cuticle of the outer surface of which is fairly strongly sclerotised and is divided into clypeus and labrum (Fig. 1a).

The posterior surface of the clypeo-labral lobe (Fig. 2c) is soft and membraneous; it forms the anterior wall of the preoral cavity and there is no sharp division between the epipharynx and the inner surface of the labrum. The epipharyngeal surface bears a double row of strong medianly directed bristles that extend as far as the mouth opening and is supported by strips of heavily sclerotised cuticle, the tormae, that arise from the basal corners of the labrum. A field of fine orally directed hairs clothes the inner surface of the labrum as far as the beginning of the bristle rows on the epipharynx. Strong bristles project from the edge of the labrum, those situated latero-ventrally have sharp bifid tips and a fringe (Fig. 2e, 2), while those within the median notch are shorter and stouter with blunt tips and several rows of spines (Fig. 2e, l), and between these two forms there are bristles of intermediate structure.

Two pairs of muscles govern the tightness with which the clypeo-labral lobe is applied to the anterior surfaces of the mandibles. Labrum retractor muscles (1) arise on the frons just lateral to the median ocellus (Fig. 1a) and are inserted by fine tendons on the proximal arms of the tormae. Labrum extensor muscles (2) arise on the frons between them and are inserted on the distal edge of the clypeus (Fig. 1a).

The mandibles

The body of each mandible (Figs. 3 & 4e) is elongated and twisted so that the outer surface of the proximal portion lies in a vertical plane parallel to the longitudinal axis of the head, while the distal portion is inflected so that its anterior surface lies in a plane transverse to the longitudinal axis of the head.

Each mandible terminates in two groups of sharp teeth, the outer and inner canines, consisting of four and two or three teeth respectively. At the base of the inner canine is articulated the prostheca that is freely movable but is provided with no muscles; that of the left mandible is stouter than that of the right and bears five teeth (Fig. 4e). Between the prostheca and molar surface of each mandible there is a thick cluster of fine hairs.

There are three positions of articulation between the mandible and the head capsule which correspond to those present in *Ecdyonurus* and *Rhithrogena*

(Strenger, *loc. cit.*). Apart from the molar surfaces and the canines, the articulatory surfaces are the most heavily sclerotised parts of the mandible.

Posterior articulation is between the ventro-lateral surface of the post gena and a strongly sclerotised surface developed on the extreme proximal end of the body of the mandible (Figs. 3d & 4e); both articulatory surfaces are long and narrow. Anterior to the articulation the base of the mandible is joined to the head capsule by an arthrodial membrane.

A thickening at a point midway along the mandible base forms the lateral articulatory surface (Figs. 3d & 4e), that fits into a grooved projection (cd) arising from the point of fusion of the anterior tentorial arm and the gena already described in the account of the head capsule.

The anterior articulatory surface is situated on the body of the mandible in the form of a blunt peg (Fig. 4e), that projects from the anterior surface so that its lateral edge rests in a slot formed by the inflected gena (Fig. 3a).

Three dorsal adductor muscles (6) (Fig. 1c) are inserted upon a tendon (t) which is attached to the dorsal anterior edge of the mandible base at the point of inflection of the distal part of the body of the mandible. The two smaller of these muscles have their origin on the vertex (6b) and the occiput (6c), while the largest, that is composed of several groups of fibres (6a), is inserted on the frons (Figs. 1a & 1c). Three bundles of tentorial adductor muscle fibres (5) originating on the body of the tentorium and the lateral surface of the base of the dorsal tentorial arm are inserted on the proximal lateral wall of the mandible body (Figs. 1c & 3d).

Abduction of the mandible is produced by two groups of muscles inserted on the base of the mandible. Two cranial abductors (3a & b) arising on the gena (Fig. 1a) and post gena (Fig. 1c) respectively, are inserted just proximal to the lateral articulatory surface (Fig. 3d). Four bundles of tentorial abductor fibres (4) lie close to those of the tentorial adductor muscles from which they may be distinguished by the position of their insertion on the basal rim and not in the body of the mandible, one bundle being anterior and the remainder posterior to the posterior articulation (Fig. 3d).

In an actively feeding larva the posterior articulatory surface of the mandible performs small movements, in a horizontal plane transverse to the long axis of the head, mainly directed to and away from the midline. The lateral articulation acts as a pivot, and as it is situated nearer to the proximal than to the distal end of the mandible, movements at the anterior articulation are of a far greater amplitude. They also take place in a different direction to those at the posterior articulation because of the twisted shape of the mandible. The anterior articulatory process slides against the thickened edge of the inflected gena in a direction approximately parallel to the long axis of the head, so that the tip of the mandible traces a complex path in which the movement of adduction includes ventral and anterior components. This movement is of great importance in feeding as the canines are made to dig against the substratum and then sweep up into the preoral cavity. The movement of the anterior articulatory process against the gena probably guides and limits the movement of the mandible to the precise direction necessary for the successful operation of the feeding mechanism.

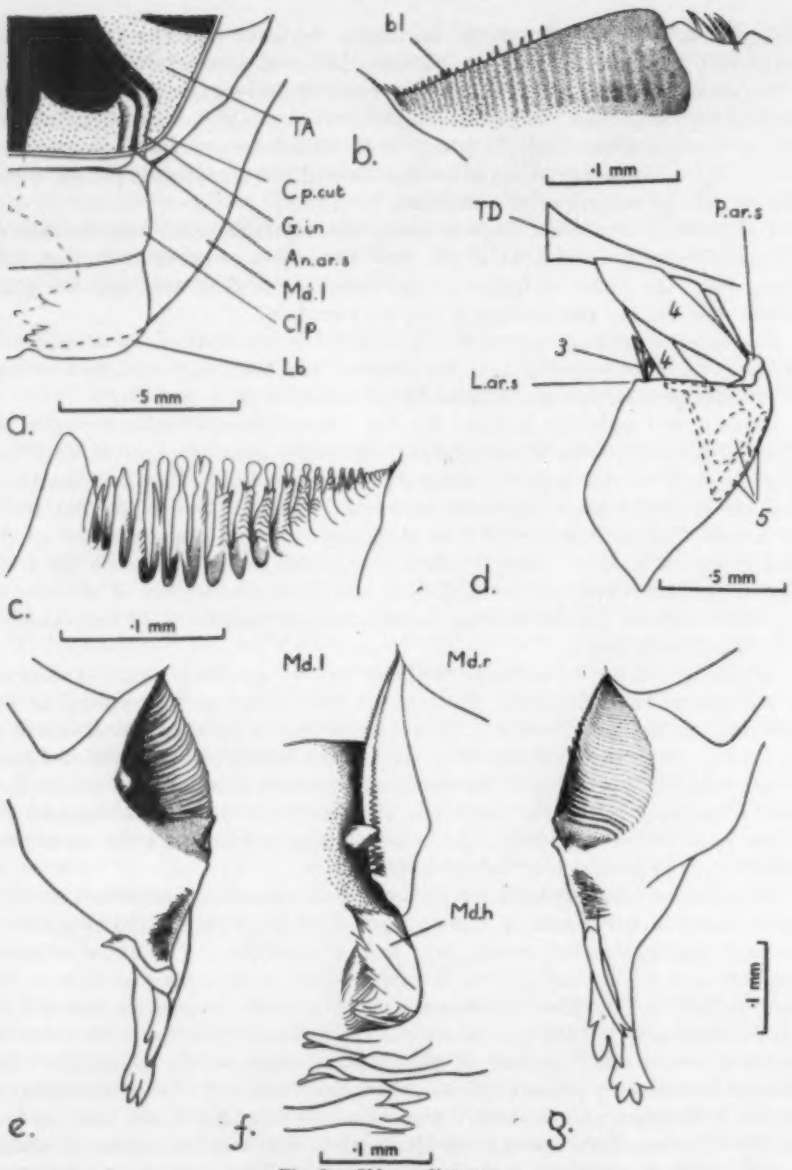

Fig. 3.—*Chloeon dipterum*

a. Head capsule. Anterior view of ventral part with wall dorsal to the epistomal suture cut away to show the anterior articulation of the mandible ; b. Molar surface of right mandible, anterior edge ; c. Molar surface of left mandible, anterior edge ; d. Left mandible. Lateral view of tentorial abductor muscles (4) ; e. Left mandible, median view ; f. Posterior view of the distal part of the mandibles in the closed position. g. Right mandible, median view. (Key to lettering, p. 175.)

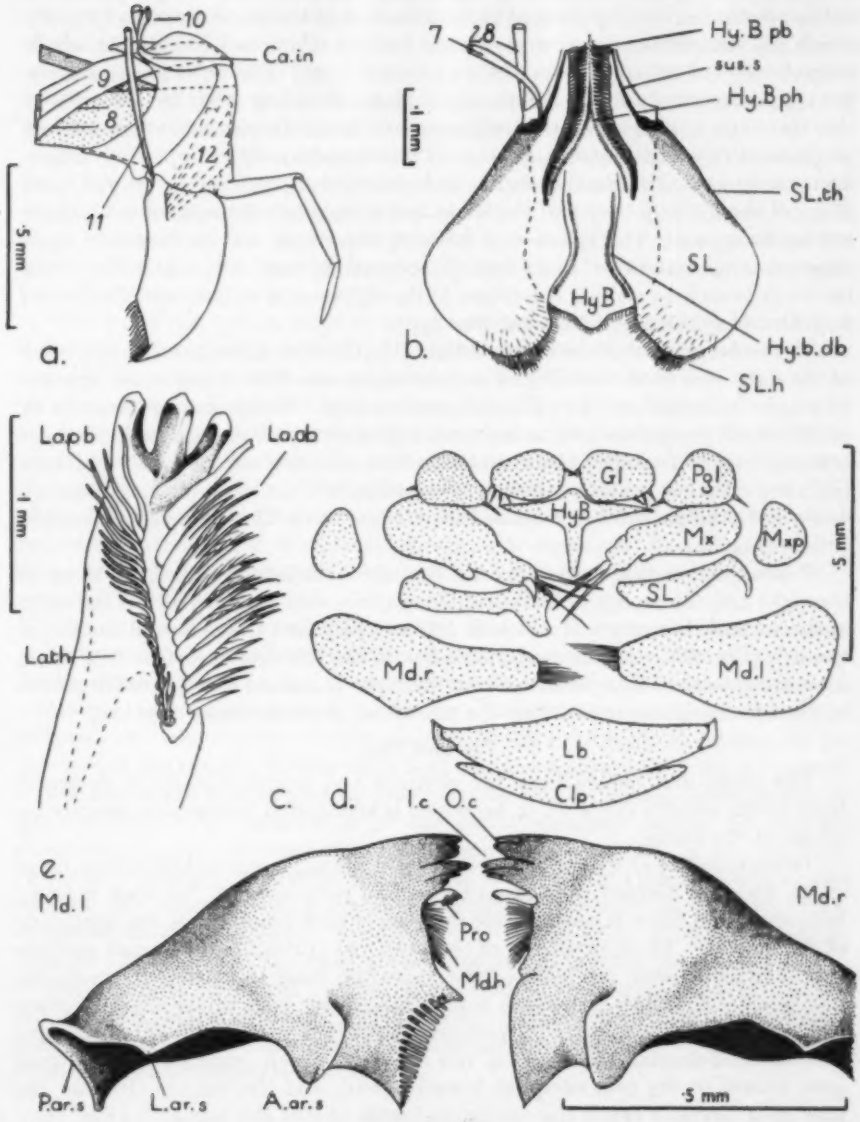

Fig. 4.—*Chloeon dipterum*

a. Left maxilla, anterior view ; **b.** Hypopharynx, anterior surface ; **c.** Tip of lacinia, median edge ; **d.** Diagram of the mouthparts in a horizontal transverse section of the head at the level of junction between the clypeus and the labrum ; **e.** Left and right mandibles, anterior surfaces. (Key to lettering, p. 175.)

Asymmetry in the structure of the mandibles, that has already been noted in the prosthecae, is very marked in the structure of the molar surfaces (Fig. 3), which are conspicuous as a result of their heavily sclerotised cuticle and which project into the proximal part of the preoral cavity. The right molar surface is covered anteriorly by a smooth edged blade of cuticle (Fig. 3b, bl). From this there run a large number of ridges that lie acros the preoral cavity and are perpendicular to the anterior surface of the mandible (Fig. 3g). The ridges decrease in size towards the mouth and are toothed; fine spines project from many of them where they join the blade and at the posterior ends of the biggest are larger spines. The spines and teeth on the ridges are sharpest and most numerous on mandibles from freshly ecdysed larvae. On mandibles from larvae approaching ecdysis the ridges of the right molar surface are often worn smooth and spines may be absent (Fig. 3g).

The molar surface of the left mandible (Fig. 3c & e) differs greatly from that of the right and when the anterior surface of the mandible is examined appears to consist of a row of stout blunt tipped prongs. Under a magnification of $\times 1450$ these prongs are seen to have a complex structure, the majority of them bearing rows of V-shaped ridges and tips that are relatively thin and spatulate (Fig. 3c). On the posterior surface of the mandible the bases of the prongs are drawn out as ridges arising from the floor of a hollow surface of heavily sclerotised cuticle (Fig. 3e).

When the mandibles are closed the canines of the left lie anterior to those of the right and the prongs of the left molar surface overlap the blade of the right molar surface, the ridges of which fit fairly closely into the hollowed surface of the left (Fig. 3f). At the posterior edge of the left molar surface is a stout conical projection that bears against the right mandible and probably serves to limit the closeness with which the mandibles can be brought together.

The maxilla

The stipes and lacinia form the elongate and antero-posteriorly flattened body of the maxilla (Figs. 1d & 4a) which is articulated to the head capsule by means of the cardo.

Great mobility of the maxilla results from the large size and structure of the cardo which is divided by a groove into two portions (Fig. 1d, Cap & Cad), between which there is considerable freedom of movement due to the flexibility of the cuticle. The median end of the proximal portion bears a small condyle that articulates with the body of the tentorium close to its junction with the post gena. A narrow projection from the anterior edge of the distal portion (Fig. 4a, Ca. in) curves under the post gena and provides the point of insertion for two cardinal-cranial muscles (10), the dorsal of which originates on the post gena lateral to the post occipital foramen (10a), and the ventral (10b) on the post gena laterally below the cranial abductor (3b) of the mandible (Fig. 1c).

While the attachment of the cardo to the stipes allows free movement between these parts there is very little freedom of movement between the stipes and lacinia. It is possible that a slight anterior movement of the lacinia tip in relation to the stipes may be produced by the contraction of the stipital-lacinial muscle (12) that passes from the postero-lateral surface of the stipes to the anterior surface of the lacinia.

From the ventral surface of the tentorium body there arise three groups of stipes adductor muscle fibres (8) that are inserted on the postero-lateral surface of the stipes, and the single cardo adductor muscle (9) inserted in the distal portion of the cardo (Fig. 1d). A single cranial lacinial muscle (11) whose origin overlies that of the dorsal cardo cranial muscle (10a) on the post gena (Fig. 1c) is inserted on the median edge of the base of the lacinia (Fig. 4a).

Movement of the first segment of the maxillary palp is brought about by a long thin protractor muscle (13) that passes from the base of the segment to the stipes, and its antagonist (14) which is short and inserted upon the lateral wall of the stipes (Fig. 1d). Protractor (15) and retractor (16) muscles pass from the base of the first to the base of the second palp segment. The terminal segment is without muscles.

The tip of the lacinia plays an important part in the gathering of food and bears a group of three prongs (Figs. 4a & 3b), two of which are movable, which are described more fully in conjunction with similar structures present in *B. rhodani*. Proximal to these the median edge of the lacinia is strongly sclerotised to support the insertions of two rows of large bristles. Those of the anterior row curve towards the labrum and are finely fringed with bifid tips (Fig. 4c, La. ab). Those of the posterior row curve towards the anterior surface of the labium and are finer and simple with sharp tips (Fig. 4c. La. pb.). The heavy sclerotisation of the bristle insertions is continued as a strengthening strip almost to the base of the lacinia (Figs. 1d & 4c) where the stipes lacinial muscle is inserted.

The movement of the maxilla is not a simple adduction and abduction in a plane transverse to the longitudinal axis of the head, but includes components in the anterior-posterior and dorsal-ventral directions so that the tip traces a complex path. Of the muscles producing adduction the strongest is the stipes adductor (8) whose origin on the tentorium lies anteriorly in relation to its insertion in the maxilla so that there is an anterior component in the movement it produces which is enhanced by the contraction of the dorsal cardinal-cranial muscle (10a). The contraction of the cardo adductor muscle (9) besides producing an anterior movement of the maxilla as a result of the anterior position of its origin relative to its insertion, brings about a straightening of the maxilla and hence a strong ventrally directed movement of the tip. This elongation of the maxilla is a consequence of the looseness of the connection between the cardo and the head capsule and the cardo and the stipes.

Abduction is produced by the contraction of the cranial-lacinial muscle (11) and the ventral cardinal-cranial muscle (10b), there being a strong dorsal component in the movement as a result of the dorsal position of the origins of these muscles in relation to the maxilla.

The labium

Cuticular attachment of the labium to the head capsule occurs by the fusion of the proximal arms of the postmentum with the post-occipital condyles on either side of the occipital foramen (Fig. 1b). A prementum is set at an angle of approximately 90 degrees to the postmentum and bears well-developed glossae and paraglossae that enclose the other mouthparts posteriorly.

The paraglossae are larger than the glossae and curve around them, their bases overlapping those of the glossae posteriorly (Fig. 1 b). A row of short, stout, anteriorly curved bristles extends along the median edge and around the tip of each glossa (Fig. 2d), and the median edges bear a row of 7–8 long straight bristles (Fig. 1b, Pgl. mb) that project over the posterior surfaces of the glossae. Long, fine hairs that presumably serve a sensory function are present on the posterior surface of both glossae and paraglossae. The glossal and paraglossal muscles arise on the distal end of an apodeme (ap) that projects from the posterior wall of the prementum ; the glossal protractors (22) being inserted on the anterior edge of the bases of the glossae, and the paraglossal extensors (21) on the lateral edge of the bases of the paraglossae (Fig. 2d).

The labial palps articulate with the postero-lateral surface of the prementum and consist of three segments, the first two being subequal and about twice as long as the third (Fig. 2d). On the dorsal surface of the tip there is a row of stout bristles that increase in length towards the tip and are interspersed with many smaller bristles and hairs ; over the rest of the surface of the palp chaetae are very sparsely distributed. No abductor muscle passes to the first segment of the palp, which is provided only with a very small adductor muscle (24) inserted on its lateral wall and arising on the posterior wall of the prementum near the median apodeme. Nearby is the origin of the large abductor muscle (23) of the second segment which is inserted on the lateral edge of the base of this segment. The adductor muscle (25) of the second segment is well developed and arises upon the posterior surface of the first segment. An adductor muscle (26) inserted on the median edge of the base of the third segment arises on the proximal lateral surface of the second segment. It was deduced from the distribution of the muscles, and directly observed in feeding animals, that movement of the labial palp is confined almost entirely to the second and third segments.

Connection between the labium and the hypopharynx in *C. dipterum* is not so close as that described by Strenger in *Ecdyonurus* ; two pairs of muscles, the posterior hypopharynx retractor muscles (19 & 20), arise on either side of the apodeme on the floor of the prementum (Fig. 2b) and are inserted on the basal sclerite of the hypopharynx body (Fig. 1d). These are probably homologous with the very large muscles that in *Ecdyonurus* extend from the hypopharynx body to the base of the labial palps (see below). They probably produce retraction of the hypopharynx because during observation of feeding larvae no movement of the base of the labium was seen. Their antagonist is the hypopharyngeal-mandibular muscle (7), which is described in the account of the hypopharynx.

Two pairs of retractor muscles of the prementum (Figs. 2b & d) originate beneath the body of the tentorium on a membrane inflected from the arms of the postmentum; the posterior retractors (17) are inserted on the apodeme and are enclosed within the arms of the postmentum, the anterior retractors (18) are inserted on the anterior edge of the prementum near the base of the palps.

The hypopharynx

In *C. dipterum* the hypopharynx forms the posterior as well as the dorsal wall of the preoral cavity (Fig. 2b). The tip of the thick, median, tongue-like

hypopharynx body (Fig. 4b) is fringed with short fine hairs, and on the anterior surface following the median edge of each superlingua is a row of fine short bristles. A conspicuous row of much larger bristles which are curved towards the median line begins near the base of each superlingua, and the two rows converge and extend, running parallel on the base of the hypopharynx body, as far as the mouth opening. Parallel and median to each of these rows of bristles is a row of hairs that are elevated on a ridge on the hypopharynx base.

The superlinguae (Fig. 4b) are flattened lobes inserted obliquely on the hypopharynx body, their lateral edges being attached at the posterior end of the suspensorial sclerite (sus. s) that supports the base of the hypopharynx body on each side. Each is capable of being pressed closely into a depression on the posterior surface of the mandible body where this is bent towards the preoral cavity, and the cuticle of the lateral edge is thickened at the point of contact (Sl. th). The lacinia fits into the space between the superlinguae and the labium on either side of the head (Fig. 2b)—the relative positions of the mouthparts as they appear in a horizontal transverse section of the head is shown in Fig. 4b. A field of relatively long fine hairs clothes the median surface of the tips of the superlinguae.

Three pairs of muscles are inserted upon the basal sclerite which is present on the posterior surface of the base of the hypopharynx body (Fig. 1d). Of these, two pairs of posterior retractor muscles (19 & 20) that arise on the posterior surface of the prementum have already been described. In addition dorsal retractor muscles (28) are inserted on the lateral basal corners of the sclerite and arise on the membrane inflected beneath the tentorium body from the arms of the postmentum (Figs. 1d & 2b). A hypopharyngeal-mandibular muscle (7) arising on the antero-lateral surface of the mandible (Fig. 1a) is inserted by means of a fine tendon on the lateral edge of the base of the hypopharynx body (Fig. 4b).

It is notable that there are three pairs of muscles (19, 20 & 28) capable of producing retraction of the hypopharynx and only one small pair (7) capable of producing protraction. This disparity indicates that when the muscles are relaxed the hypopharynx lies closely pressed forwards against the mandibles and that after contraction of the retractor muscles it returns to this position as a result of the elasticity of its cuticle and perhaps also the pressure of the internal fluids of the head capsule within the lobes. It is likely that the hypopharyngeal-mandibular muscle is responsible for drawing the hypopharynx tightly against the posterior surface of the mandibles while swallowing takes place.

THE FUNCTIONING OF THE MOUTHPARTS OF *CHLOEON DIPTERUM*

When feeding upon fine detritus

Both the rate of activity of the mouthparts as a whole and the rate and direction of movement of particular parts in relation to the others varied according to the kind of food being ingested. The mechanism employed when the larvae were feeding upon a fine loose detritus was that most frequently observed in captivity and is described in detail below. A brief account follows

of the ways in which this mechanism is modified to deal with a more aggregated detritus, rotted higher plant tissue, and filamentous algae.

When the head is viewed from the ventral or anterior aspects, it is seen that there is a regular alternation between the mandibles and maxillae in their inward and outward movements. Fig. 7a, 1 shows these mouthparts in the resting position. At the commencement of feeding the laciniae move inwards and the mandible tips move outwards to the position shown in Fig. 7a, 2. The mandibles are then closed and their tips brush against those of the laciniae at position X in Fig. 7a, 3. The mandibles are brought more closely together than in the resting position so that the tip of the left lies anterior to and overlapping that of the right (Fig. 7a, 3). As the mandibles now move apart the laciniae are brought together so that they occupy the position shown in Fig. 7a, 2, and from this position the sequence of movements is repeated at a rate varying from 10 to about 250 times per minute, for periods of up to four minutes.

Food is collected by the activity of the labial palps, laciniae and mandible tips. When fine detritus is provided as food the labial palps move more quickly than the mandibles and maxillae and perform rapid flicking movements by which food particles caught in the bristles are brushed towards the preoral cavity. They are swept further into the preoral cavity by the laciniae which gather particles directly from the substratum both by means of bristles on the median edge and the terminal claw. The laciniae play the most important part in food collection, the mandibles rarely being used for this purpose when the detritus is fine and loose.

It is impossible to observe directly the mechanism by which fine detritus swept into the preoral cavity by the laciniae is held there and swallowed, and the following account of this process is deduced from the structure of the mouthparts and their known movements. While for descriptive purposes it is assumed that the head is held with its long axis approximately vertical so that the force of gravity is opposing the passage of the food to the mouth opening, this is not the only position in which the larva feeds; larvae have in fact been observed feeding in a great variety of positions and it is probable that the orientation of the head has no effect on the successful functioning of the feeding mechanism.

Each inswinging lacinia passes between the superlingua and the hypopharynx body and food is deposited between the tips of the hypopharynx lobes and the edge of the labrum, (position X Fig. 7b). It is retained in this position when the laciniae withdraw by the bristles of the glossae and the paraglossae, the edge of the labrum, and the fine hairs on the tips of the hypopharynx lobes. As the laciniae withdraw they must pass once more between the superlinguae and the hypopharynx body and any food particles adhering to the bristles are removed, probably mainly by the lateral rows of bristles on the hypopharynx body (Fig. 4b, Hy. b. db.). The hypopharynx is probably retracted when the laciniae move inwards thus enabling them to pass more easily between the lobes and enlarging the preoral cavity to receive the food.

As the mandibles are closed the superlinguae press tightly into the grooves on their posterior surfaces and the hypopharynx as a whole is probably drawn

forwards by the contraction of the hypopharyngeal-mandibular muscles (7). In this way the volume of the ventral part of the preoral cavity would be reduced and the food, being unable to pass ventrally out of the preoral cavity because of the tips of the hypopharynx lobes and the canines of the mandibles, would be forced towards the mouth. Further, the direction of movement of the mandibles as they close is such that the food within the preoral cavity tends to be swept towards the mouth by the canines, hairs, and prosthecae. The fine hairs on the posterior surface of the labrum, being dorsally directed, serve to prevent food particles from falling ventrally. A dark mass of food appears to fill completely the preoral cavity of an actively feeding larva when food is abundant, and it would seem that an important factor tending to force food towards the mouth under these conditions is the pressure of the new food that is continually being introduced into the preoral cavity. Swallowing is probably aided by the closing of the molar surfaces which occupy the dorsal part of the preoral cavity, that of the right mandible projecting slightly into the mouth. The shape of the molar surfaces is such that as they close the intervening space between them is reduced progressively in a ventral-dorsal direction, so that any food lying between them is displaced to the mouth.

It is to be expected, in view of the disturbance of the osmotic properties of the body fluids and the dilution of the digestive enzymes that would result from the ingestion of large quantities of water, that the food is swallowed in a relatively dry condition. This view is supported by the tightness into which food is found to be packed into the foregut of an actively feeding larva. From a consideration of the structure of the molar surfaces it may be concluded that they are adapted to performing a straining as well as the grinding function usually attributed to them. As the mandibles close, water is free to pass between the large bristles of the hypopharynx body and those on the epipharynx, and between the prongs of the left molar surface, but food particles will be retained by these structures. Only when the prongs of the left molar surface have completely overlapped the blade of the right molar surface (Fig. 3f), and no more water can be expelled between them, will the food be subjected to the crushing action of the molar surfaces.

The passage of food consisting of fine detritus to the mouth may be summarised as follows—

1. Food collected by the labial palps, laciniae, and occasionally the tips of the mandibles.

2. Food swept into the preoral cavity by the laciniae, the hypopharynx being retracted.

3. Food retained in the ventral part of the preoral cavity by the bristles or hairs situated on

   i. the labrum edge.

   ii. the inner surface of the labrum.

   iii. the glossae and paraglossae.

   iv. the tips of the hypopharyngeal lobes.

4. Food forced towards the mouth by the mandibles as they close and the pressure produced by the protraction of the hypopharynx.

5. Food prepared for swallowing by the straining and crushing action of the molar surfaces, being held in position between them by the bristles of the epipharynx and the hypopharynx body.

When feeding upon other food materials

When larvae were feeding upon filamentous algae, aggregated detritus or vascular plant tissue, the mandibles played a more important part in the collection of food then when this was fine detritus. Larvae were observed to bring the tips of the mandibles to bear upon the food by lowering the head, and the small fragments broken off by the canines were brushed into the preoral cavity by the other food collecting appendages. Filaments of algae were drawn continuously into the preoral cavity by deliberate chewing movements of the mandible. On one occasion the mandible tips were seen to actually bite short pieces from a stout filament of *Spirogyra*.

The movements of the other mouthparts in relation to the mandibles during the ingestion of these food materials were the same as those described for the ingestion of fine detritus. It was the rate of movement of the mouthparts as a whole, and the extent to which the mandible tips were used as food collecting organs, that varied with the type of food.

The rate of movement of the mouthparts

The number of complete cycles of inward and outward movements made by the mandibles and maxillae in 30 second periods was counted in several large larvae. Three distinct rates of movement occurred that were correlated with the nature of the food.

In the case of larva feeding upon a coarsely aggregated detritus the deviation from a mean rate of 68 movements/30 secs. was slight, i.e., for five individuals the extreme valves observed were 65 and 70 movements/30 secs. Larvae brushing up fine detritus from the surface of the filaments of algae or vascular plants showed a far higher rate of movement that was difficult to count because of its rapidity. It was approximately four times as great as that observed in larvae feeding upon aggregated detritus.

The slowest rates of mouthpart movement, 10–30/30 secs., were recorded when larvae were ingesting filaments of algae.

The part played by the limbs

Larvae climbing amid vegetation or loose detritus were occasionally seen to draw material towards the head with the forelimbs but it is probable that this occurred by chance in the normal process of locomotion. On several occasions larvae were observed to remove material adhering to the bristles of the legs by drawing the leg through the mouthparts in a manner that was reminiscent of the behaviour described in *Habrophlebia lauta* McLach. and *Habroleptoides modesta* Hagen by Pleskot (1953). In *H. modesta* the forelimbs performed sweeping movements, and pieces of detritus caught in the thick field of serrated bristles on the tibiae were passed forwards to the mouthparts by a deliberate movement of the limbs, or held fast by retracting the tibia closely against the femur. Pleskot suggests that the resemblance between the long

hairs upon the fore tarsus and those on the labial palps is the result of parallel adaptation to food collection. None of the limbs of *Chloeon dipterum* bear thick fields of bristles that would be obviously suitable for food collection, and although food may be taken by the mouthparts from the limbs as described above, this is not a regular part of feeding behaviour and appears to be an accidental means of food collection in this species. The prime purpose of the action observed in *C. dipterum* appeared to be to free the limb of encumbering material and the origin of the kind of behaviour described by Pleskot may lie in cleaning actions of this kind.

Autocoprophagy, a phenomenon rarely recorded in insects, was observed in both *Habrophlebia lauta* and *Habroleptoides modesta* by Pleskot. In the former species, faecal pellets were deliberately caught by passing the posterior end of the abdomen through the crook between the tibia and femur of the foreleg and conveyed to the mouthparts. In *H. modesta* pellets were collected by the hind leg and passed forwards to the tibial bristles of the middle leg and thence to the bristles of the fore tibia and the mouthparts. In *C. dipterum* this was not observed but occasionally a larva, irritated by the presence of a particle of detritus on the cerci, would bend the abdomen forwards and quickly brush the cerci against the mouthparts so that the particle was removed. Again, in *C. dipterum* there appeared to be a possible origin of behaviour far more highly developed in other species of ephemeropteran larvae.

THE MORPHOLOGY OF THE MOUTHPARTS OF *BAETIS RHODANI*

The head capsule

In general appearance the head capsule of *B. rhodani* resembles that of *C. dipterum*, differing from it mainly in the relative proportions of various parts and in the generally greater sclerotisation of the cuticle. The ocelli and antennae are situated more ventrally so that the upper part of the head capsule consists of a large expanse of smoothly curved vertex and is well adapted to present only slight resistance to flowing water (Fig. 5a). Adaptation to the same end is seen in the posterior wall of the capsule which is hollowed so that the margins slightly overlap the prothorax and the head and thorax together present a streamlined shape to the water.

As in *C. dipterum* only coronal, frontal, and epistomal sutures are visible and there is no definite boundary between the frons and the lower part of the gena and between the posterior part of the vertex and the occiput (Figs. 5a & 6b). Muscles inserted on the mouthparts are attached to the head capsule in similar positions in the two species. The dorsal arm of the tentorium is attached to the cranium in a more ventral position in *B. rhodani*.

The clypeo-labral lobe

The labrum is relatively narrower than that of *C. dipterum* but it forms an effective anterior wall to the preoral cavity because of the elongated and tapered shape of the distal parts of the mandibles and maxillae. The posterior surface of the labrum is strongly concave and as a result of the thickening of the cuticle of the outer wall, particularly at the edges, it is difficult to bend the labrum away from the preoral cavity.

Well-developed tormae (Fig. 6e) support an epipharyngeal surface that bears long bristles arranged in two asymmetrical rows. The longer arms of the tormae are asymmetrical in correlation with these bristle rows which merge into fields of short fine bristles that extend to cover a median raised area on the surface of the labrum. On either side of the apex of the posterior surface of the labrum is a field of medianly directed hairs.

The bristles of the labrum edge are distributed in three rows (Fig. 8f); a row of simple bristles on the lateral edges extends on to the anterior surface, basally the bristles of this row are interspersed with fringed bristles which are confined to the edge and are situated nearer the posterior surface, apically these are succeeded by stouter fringed bristles that are set close together beneath a flange of cuticle.

The labrum protractor muscles (2) arise on the frons ventral to the median ocellus and are inserted basally on the outer wall of the labrum. Retractor muscles (1) arise on the frons on either side of the protractors and are inserted by fine tendons on the shorter arms of the tormae.

The mandibles

The tip of the mandible is more tapered than in *C. dipterum*, and the straight canines project towards the substratum rather than into the preoral cavity (Fig. 5d). The inner canine is composed of several blunt teeth but the outer shows only traces of subdivision. Asymmetrical prosthecae are present, that of the left mandible bearing four blunt teeth and three long bristles while that of the right is comparatively slender and terminates in a cluster of fine hairs (Fig. 5d).

Three groups of muscle fibres, originating on the frons (6a), the vertex (6b) and the occiput (6c), form the dorsal adductor muscle (Figs. 5a & 6b). Three groups of tentorial adductor muscle fibres (5) originate on the body and base of the dorsal arm of the tentorium and are inserted on the lateral surface of the mandible. Two cranial abductor muscles (3a & 3b) arising on the gena and post gena respectively (Figs. 5a & 6b), are inserted on the mandible base just posterior to the lateral articulation, and two tentorial abductors (4) that arise on the base of the anterior tentorial arms are inserted on the mandible anterior to the posterior articulation.

On examination of the anterior surface of the right mandible, the edge of the molar surface is seen to consist of a blade of heavily sclerotised cuticle similar to that of *C. dipterum*, beyond which project the tips of blunt tubercles (Fig. 7c). These are the biggest of the large number of tubercles of cuticle that cover the whole of the molar surface, increasing in size towards the posterior edge where they are arranged in rows (Fig. 7d). A few sharp spines are present at the end of some of the rows in the same position as they occur in *C. dipterum*.

The anterior edge of the left molar surface consists of a row of curved prongs (Fig. 7e), resembling those of *C. dipterum* but lacking ridges and spatulate tips. Large numbers of tubercles of cuticle cover the adoral part of the surface, and there is a row of sharp bristles on the posterior edge (Fig. 7f). A large blunt peg occupies a similar position as in *C. dipterum*,

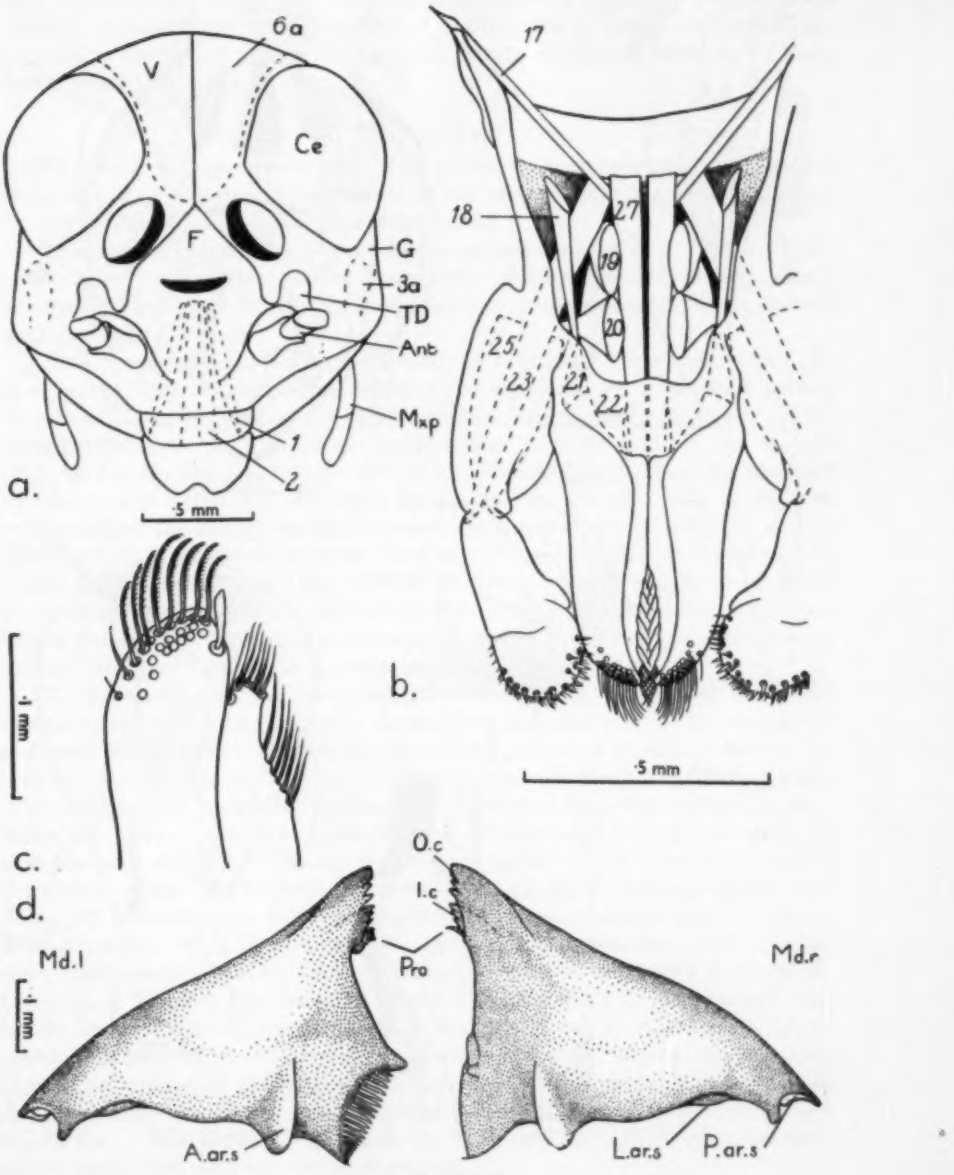

Fig. 5.—*Baetis rhodani*

a. Head capsule, anterior surface ; b. Labium, anterior surface ; c. Tips of glossae and paraglossae. Anterior surface (only the distal row of paraglossal bristles shown) ; d. Left and right mandibles, anterior surfaces. (Key to lettering, p. 175.)

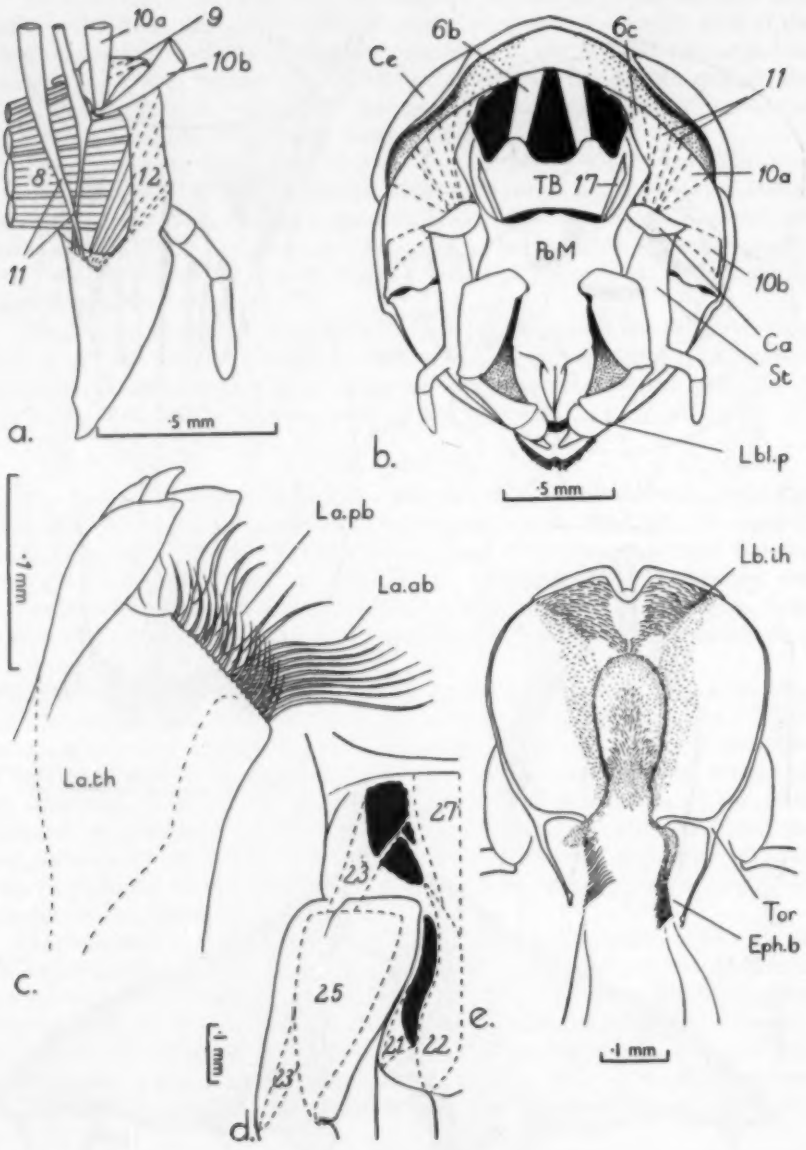

Fig. 6.—*Baetis rhodani*

a. Left maxilla, anterior surface ; b. Head capsule. Posterior surface, oesophagus and cervical muscles removed ; c. Tip of lacinia. Oblique view of posterior surface ; d. Labium. Posterior view, including the basal segment of the palp showing the distribution of the muscles ; e. Clypeo-labral lobe, posterior surface. (Key to lettering, p. 175.)

and when the mandibles are closed projects over the edge of the right molar surface, probably serving the purpose of limiting the tightness with which the mandibles are closed and preventing damage to the molar surfaces by their being ground together.

The maxillae

The body of the maxilla (Fig. 6a), which is more compact and tapered than that of *C. dipterum* is articulated to the head capsule in a similar manner by the proximal part of the subdivided cardo.

Two rows of bristles are present on the lacinia tip (Fig. 6c). Those of the posterior row are simple, but of the anterior row only the three large distal bristles are bifid and fringed as in *C. dipterum*, the remainder being slender and relatively far longer.

In *B. rhodani* each lacinia terminates in four claw-like prongs (Figs. 8a & c) resembling the three that occur in *C. dipterum*, of which that arising from the posterior surface (1) is immovable, its heavily sclerotised cuticle being continuous with the thick strip in the posterior wall of the lacinia (Fig. 6c, La. th, Fig. 8a, P.th). Of the movable prongs, that on the anterior surface of the lacinia tip (4) is the largest and its rounded base articulates with a slight thickening in the anterior wall of the lacinia (Fig. 8a, a. th). The two lateral prongs (2 & 3) are smaller with less heavily sclerotised cuticle which is continuous with that of the lacinia so that there is no definite articulation at their bases. When the claw of the lacinia is closed the two lateral prongs fit closely together between the anterior and posterior prongs so that the tip of the lacinia is scoop shaped (Fig. 8e).

The functioning of the tip of the lacinia, which in appearance resembles certain types of mechanical grab, depends on the elasticity of the cuticle at the bases of the prongs, as there are no muscles present in the distal part of the lacinia. While the maxilla is inactive the prongs are closed but as the lacinia is brought to bear on the substratum the pressure causes them to splay open. When the lacinia is retracted they close again and tend to grip any material that has been dislodged from the substratum which is then conveyed towards the preoral cavity. In *C. dipterum*, while the cuticle of the posterior immovable prong (1) is continuous with the thickening in the posterior wall of lacinia as in *B. rhodani* (Fig. 8b), the two other prongs (2 & 3) can move and a similar scoop-like structure can be formed. There is, however, no clearly demarcated articulation between the bases of either of these movable prongs and the lacinia as is present at the base of the anterior prong in *B. rhodani*. It is possible that the three prongs of *C. dipterum* are homologous with the posterior and lateral prongs of *B. rhodani* and that the anterior prong in this species should be regarded as a greatly enlarged bristle of the anterior row on the lacinia tip. This bristle (Figs. 4a & 8b, 4) is very large in *C. dipterum* and closely associated with the terminal prongs.

The arrangement of the muscles in the maxilla closely resembles that in *C. dipterum* and produces a similarly complex movement. Stipes and cardo adductor muscles (8 & 9) arise on the lateral surface of the tentorium body and base of the anterior tentorial arm and are inserted on the postero-lateral surface

of the maxilla (Fig. 6a). Two parts of the cardinal-cranial muscle, arising on the dorsal (10a) and the lateral (10b) parts of the post gena (Fig. 6b), are inserted on the inflected distal part of the cardo (Fig. 6a). The cranial-lacinial muscle (11) is relatively more strongly developed than in *C. dipterum*, it is divided into two parts arising on the dorsal wall of the post gena (Fig. 6b) and inserted by fine tendons on the anterior edge of the base of the lacinia (Fig. 6a). A well developed stipital-lacinial muscle (12) is present although the possible movement between the stipes and lacinia appears to be very slight.

When fully extended the maxillary palp does not extend to the tip of the lacinia, being relatively shorter than that of *C. dipterum*, which it resembles in bearing a few short hairs only. The first and second segments are provided with protractor and retractor muscles that are uncrossed as in *C. dipterum*.

The labium

The glossae, paraglossae, and the prementum (Fig. 6b) are relatively longer than in *C. dipterum*, and, as a result of the posterior inclination of the mouth-parts, the angle between the postmentum and the prementum is not so acute. There is close contact between the narrow glossae and the hollowed median edges of the paraglossae (Figs. 5b & c). The median edges and tips of the glossae bear long bristles, and stouter medianly curved bristles are distributed on the anterior surface of the tips of the paraglossae in three rows (Fig. 5c). A magnification of $\times 950$ reveals a fine fringe on these bristles. One bristle situated on the median edge of the tip of the paraglossa is sharply differentiated from the others being short and stout with a blunt tip (Fig. 5c). No such structure is present in *C. dipterum* and the significance of its occurrence in *B. rhodani* is at the present time obscure. Well developed muscles (Fig. 6d) pass from the prementum to the glossae (22) and paraglossae (21). As a result of the lateral position and small area of their insertions these muscles must produce a movement of extension rather than protraction which appears to be their function in *C. dipterum*. No antagonistic muscles are present and the elasticity of the cuticle must be presumed to play an important part in the functioning of the glossae and paraglossae.

The labial palps are articulated to the lateral posterior surface of the prementum (Figs. 6b & d). Their bases are stouter than those of *C. dipterum*. The third segment is rounded, and its articulation with the second segment is incomplete; distally it bears many fine hairs and curved bristles (Fig. 5b). There is no trace of either the small adductor muscle (24) of *C. dipterum* or of a muscle passing from segment two to segment three. The movement of the palp is brought about entirely by the abductor (23) and adductor (25) muscles, inserted on the base of the second segment and arising on the posterior wall of the prementum and the posterior base of the first segment of the palp respectively (Fig. 6d).

Two posterior hypopharynx retractor muscles (19 & 20), inserted on the basal sclerite of the hypopharynx body, arise on the posterior wall of the prementum as in *C. dipterum* (Fig. 5b).

Posterior (17) and anterior (18) prementum retractor muscles are inserted on the prementum in similar positions as in *C. dipterum* but the former arises

on the posterior surface of the tentorium body (Fig. 6) and does not pass beneath it.

A pair of muscles (27) which is absent in *C. dipterum* arises on the basal posterior surface of the prementum and is inserted close to the bases of the glossae (Fig. 5b). The cuticle of the prementum is not strongly sclerotised and the contraction of these large muscles probably produces an anterior movement of the distal part of the labium relative to the base which presses it closely against the other mouthparts.

The hypopharynx

A well developed hypopharynx is present consisting of a tongue like body and lateral superlinguae, which are elongated in comparison with those of *C. dipterum* and are more densely covered with chaetae (Fig. 8d).

Almost the entire anterior surface of the distal part of the hypopharynx body is occupied by fields of hairs, of greatest length and density near the tip, that converge upon the mid-line and are directed towards the mouth. Proximally there are two rows of stout medianly curved bristles, with parallel rows of fine hairs, that are very similar to those of *C. dipterum*.

The cuticle of the lateral edges of the superlinguae is relatively heavily sclerotised proximally where the superlinguae fit closely against the posterior surfaces of the mandibles as in *C. dipterum*. Their tips bear a dense field of fine hairs.

Two posterior retractor muscles (19 & 20), that have already been described, are inserted on the basal sclerite of the hypopharynx body on the corners of which are inserted a pair of dorsal retractor muscles (28) arising beneath the body of the tentorium. As in *C. dipterum* a hypopharyngeal-mandibular muscle (7) passes from the suspensorial sclerite in the lateral edge of the hypopharynx body to the lateral wall of each mandible.

THE FUNCTIONING OF THE MOUTHPARTS OF *BAETIS RHODANI*

The movements of the mouthparts closely resembled those of *C. dipterum* in that the mandibles and maxillae performed regular alternating movements and food was collected by the labial palps, laciniae, and mandible tips.

In general the rate of movements was slower than in *C. dipterum* and at all times the mandibles were brought to bear upon the food. Larvae of *B. rhodani* were observed feeding upon detritus and a mixture detritus and diatoms adhering to the surfaces of stones, but could not be induced to feed upon filamentous algae. On no occasion did larvae brush up fine detritus solely by means of the labial palps and the laciniae as frequently occurred in *C. dipterum*.

The greater importance assumed by the mandibles in food collection in *B. rhodani* is probably necessitated by the difficulty of dislodging particles of detritus and diatoms from the surface of stones in streams. The crouching stance assumed by larvae of *B. rhodani* when feeding serves to thrust the mouthparts close against the substratum, as well as preventing the animal being swept away by the current.

THE RELATIONSHIP OF THE DIFFERENCES IN THE MOUTHPARTS BETWEEN *C. DIPTERUM* AND *B. RHODANI* WITH THEIR HABITATS

There are a few differences between the mouthparts of *C. dipterum* and *B. rhodani* of which the functional significance is not clear, but the majority of the morphological characteristics of *B. rhodani* are consistent with the overall adaptation of this species to flowing water.

Larvae of the genus *Baetis* are among the most active of the insect larvae occurring in flowing water, they are frequently seen on the tops of stones, swim rapidly when disturbed, and rely on their stream-lined shape to keep them from being swept away down stream. The effects of streamlining on the head capsule are seen in the ventral positions of the antennae and ocelli, the large expanse of smoothly curved vertex, and the indentation of the posterior wall of the capsule so that the edges overlap the prothorax.

Three different effects of streamlining appear in the structure of the mouthparts. Firstly, the surface area of the distal parts of the mandibles and maxillae is reduced by their tapered shape; the glossae, paraglossae, and the hypopharynx body being correspondingly elongated to form an effective posterior wall to the preoral cavity. Secondly, a reduction of bristles and hairs in places where they are not essential for retaining food particles is seen in the glossae and paraglossae which, apart from their tips, are devoid of chaetae. Reduction of the length and mobility of the appendages so that they do not move outside the area sheltered by the front margin of the head is a third means whereby the resistance offered to the water by the mouthparts is reduced, and is characteristic of the extremely flattened forms of mayfly larvae; such adaptation is present in *B. rhodani* in the shortness of the labial and maxillary palps and the absence of a muscle in the third segment of the former.

The body of an animal living in flowing water is exposed for most of its life to physical stresses that are absent in a pond, and the general appearance of the head capsule of *B. rhodani* is more robust than that of *C. dipterum*, the sclerotisation of the cuticle, particularly of anterior surface and edges of the labrum, being relatively greater. The glossae and paraglossae fit far more closely together than in *C. dipterum* and are supported by wide bases, those of the paraglossae overlapping those of the glossae posteriorly, so that they are not easily forced away from the preoral cavity. It is likely that the pair of muscles (27), present in the prementum of *B. rhodani* and absent in *C. dipterum*, is a further adaptation to strengthen the labium and brace it against the preoral cavity.

Besides the direct effect described above, flowing water exerts an indirect influence on mouthpart morphology through the effect it has in the food both before and after this is collected. Encrusting organisms are firmly attached to the substratum in a stream and detritus is confined to small crevices where the flow is at all rapid. The mechanical difficulties of food collection are thus greater than in a still water habitat and even when material has been dislodged it may be swept away by the current before reaching the mouth. Several of the details in which the mouthparts of the two species differ appear to be correlated with these difficulties. The blade-like outer canine of *B. rhodani* is better fitted to dislodge epilithic algae and encrusting particles than the sharp

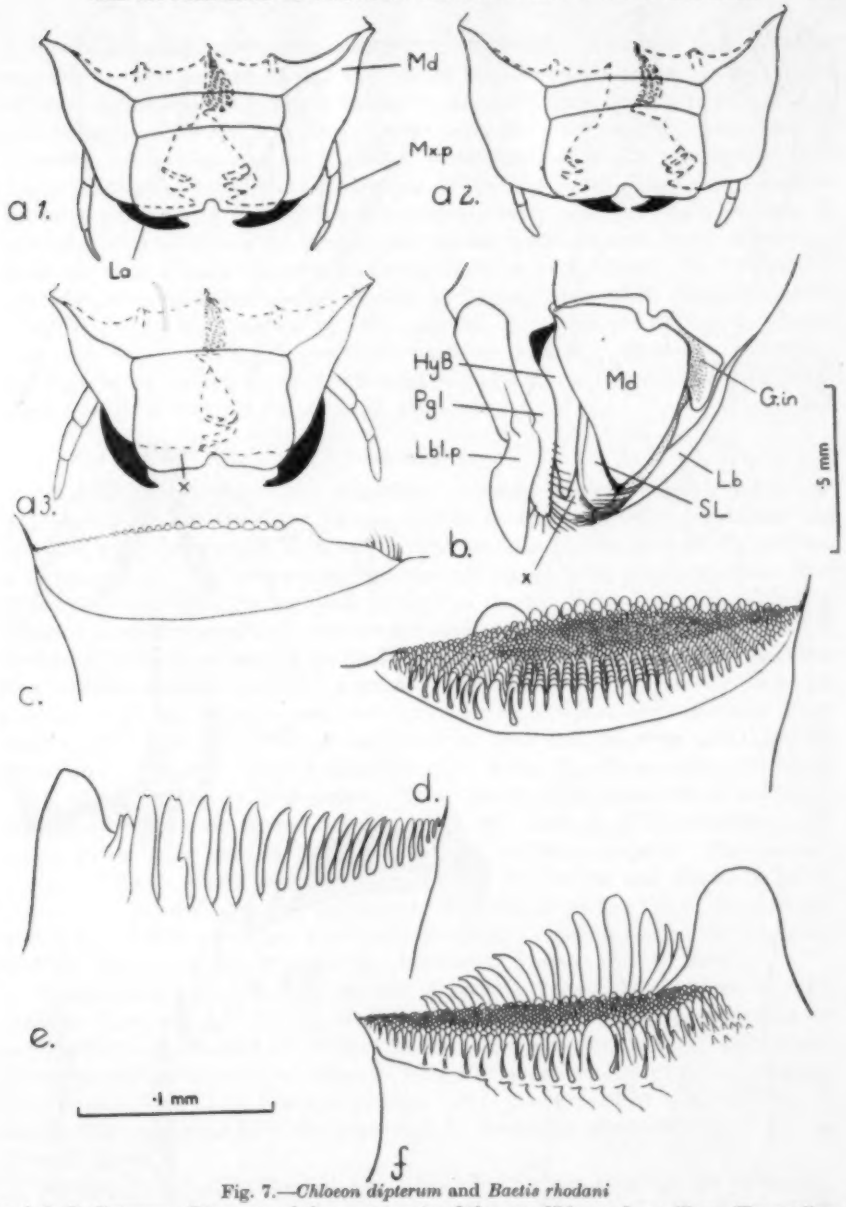

Fig. 7.—*Chloeon dipterum* and *Baetis rhodani*

a. 1–3. *C. dipterum*. Diagrams of the movements of the mandibles and maxillae. The outline of the mandibles is shown through the clypeo-labral lobe and the ventral part of the anterior surface of the head capsule ; b. *C. dipterum*. Lateral view of the mouthparts, right maxilla removed ; c. *B. rhodani*. Right molar surface, anterior edge ; d. *B. rhodani*. Right molar surface viewed obliquely from the posterior surface of the mandible ; e. *B. rhodani*. Left molar surface, anterior edge ; f. *B. rhodani*. Left molar surface, viewed obliquely from the posterior surface of the mandible. (Key to lettering, p. 175.)

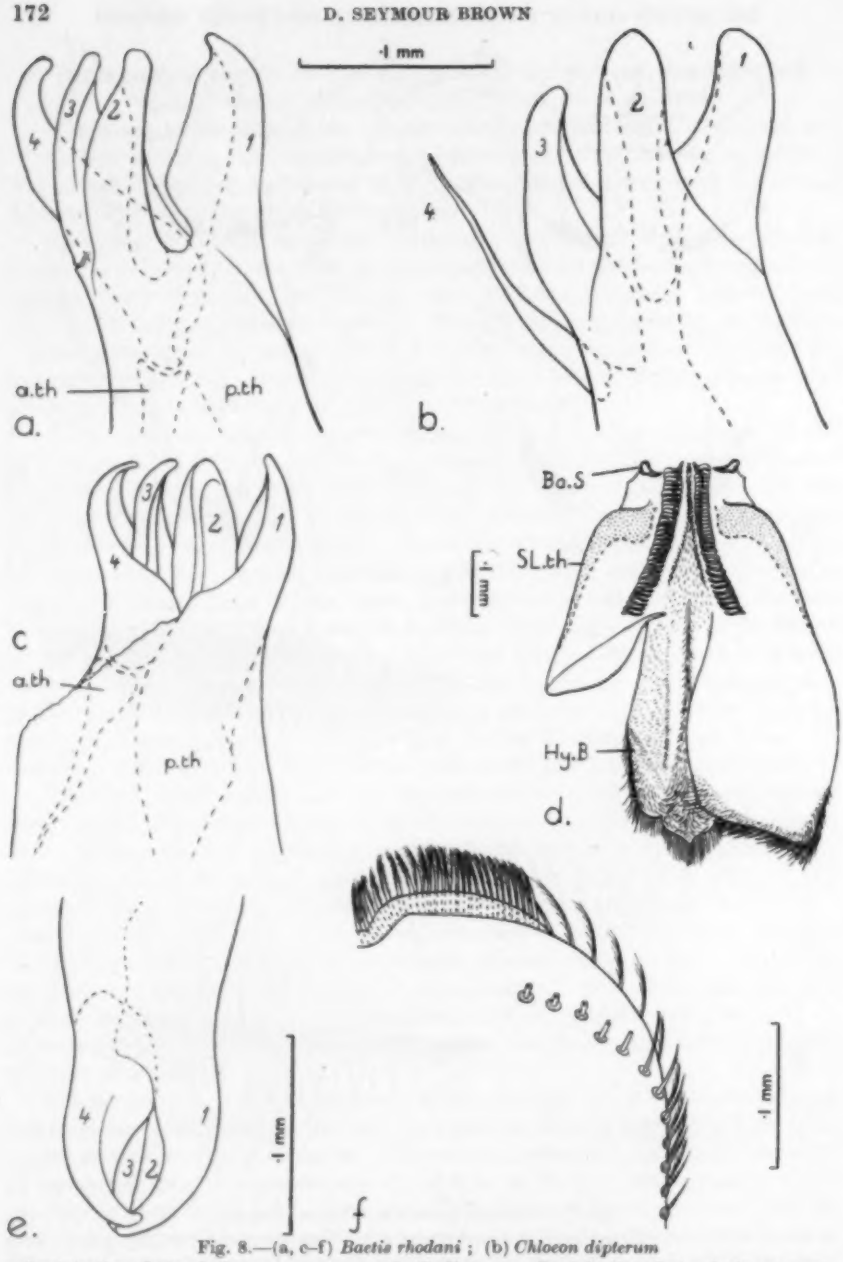

Fig. 8.—(a, c–f) *Baetis rhodani* ; (b) *Chloeon dipterum*

a. Lacinia tip. Lateral view, prongs open ; b. *C. dipterum*. Lacinia tip. Lateral view, prongs open ; c. Lacinia tip. Median view, prongs open (bristles omitted) ; d. Hypopharynx. Anterior surface, right superlingua removed ; e. Lacinia tip. Median view, prongs closed ; f. Labrum. Posterior view of edge. 1. Posterior prong of lacinia tip ; 2 & 3. Lateral prongs of lacinia tip ; 4. Anterior prong of lacinia tip (*B. rhodani*). Distal bristle of anterior row (*C. dipterum*). (Key to lettering, p. 175.)

points of the subdivided outer canine of *C. dipterum*. A lacinia with a greater number of more mobile prongs and longer bristles would also serve as a more efficient food collecting organ under these conditions. Greater complexity and strength in the molar surfaces, particularly the presence of large numbers of tubercles of cuticle, may be regarded as adaptation to the more gritty and finely particulate food that is deposited by flowing water. Adaptation to the function of retaining food within the preoral cavity is present in *B. rhodani* in the form of the thick chaetation in the anterior surfaces and tips of the hypopharynx lobes and the inner surface of the labial-epipharyngeal lobe. Similarly the bristles of the labrum edge, glossae, and paraglossae of *B. rhodani* are well adapted to prevent the loss of food particles from the preoral cavity, being relatively longer and more closely set together than in *C. dipterum*. Further, the fringing of the labral bristles is thicker and a fringe is present on the paraglossal bristles that are simple in *C. dipterum*.

DISCUSSION

The feeding mechanisms described provide several examples of the importance of the elasticity of the cuticle in the relationship between the skeleton and the muscles in insects. This is seen particularly in the labium and hypopharynx where several muscles act singly with no antagonists, and in the functioning of the movable prongs on the tip of the lacinia in which no muscles at all are present. Structures similar to the prongs described on the lacinia of *C. dipterum* and *B. rhodani* are also present in the closely related genus *Centroptilum* and are obviously a suitable adaptation of mayfly larvae in which the tips of the mouthparts are used to collect food. However, the only other genera, of which figures of the lacinia have been examined, in which similar structures occur are *Epeorus* (Lestage 1921, after Eaton) and *Iron* (Morgan, 1911) of the family Heptageniidae. These are both flattened forms and their mouthparts resemble those of *Ecdyonurus*, the surfaces of the maxillary and labial palps being greatly enlarged as food collecting organs. The lacinial prongs of *Epeorus* and *Iron* differ from those of *Chloeon* and *Baetis* in being borne on a separate process apparently articulated to the tip of the lacinia, and it is probable that they have been acquired independently in the Baetidae and the Heptageniidae, functioning in different ways in the two families.

Many specimens of *C. dipterum* and *B. rhodani* approaching ecdysis showed marked signs of wear in the molar surfaces. Very few other examples of mechanical deterioration of the hard parts have been recorded in invertebrates. Those occurring in mature animals, where they are an aspect of senescence, have been reviewed by Comfort (1954). It is probable that the efficiency of the feeding apparatus in *C. dipterum* and *B. rhodani* is impaired in aged larvae of each instar.

Murphy (1922) attempted to group the molar surfaces of larval Ephemeroptera into three types, and describes rounded and knobbed transverse ridges as the prevailing type among the Baetinae that inhabit streams with sand or gravel bottoms. The molar surfaces of *B. rhodani* differ from this description in the presence of a multitude of tubercles and conspicuous processes on the anterior edge of the left surface. It is probable that future work will show

Murphy's classification to be far too simple. The molar surfaces of *B. rhodani* and *C. dipterum* show constant differences in the details of their structure, which can be partly explained by reference to the composition of the diet, and further study may reveal precise specific correlation between the morphology of the molar surfaces and the diet in many species of ephemeropteran larvae. Such specialisation will be most obvious in those forms in which the food is relatively homogeneous. For example, the laciniae of several flattened rapid water genera are equipped with stout comblike bristles that are adapted to rake up the diatoms that form the major part of the food, e.g., *Ameletus* (Schoenemund 1930), *Stenonema pulchellum* (Trama, 1957) and *Rhithrogena* (Strenger, 1953). The feeding mechanism of *C. dipterum* and *B. rhodani* is adapted to allow the ingestion of a heterogeneous diet in a wide variety of habitats, and hence structures that can be related to the ingestion of a particular food component are absent.

The study of the feeding mechanism of *C. dipterum* and *B. rhodani* has added to the already great diversity of mouthpart morphology described in larval Ephemeroptera, and, as a result of combining dissection with direct observation of the feeding mechanism, it has been possible to establish or suggest the functional significance of many anatomical features. In view of this it seems likely that similar studies of more species will result in a general understanding of the morphology and functioning of the feeding apparatus within the Order, and of the ways in which the various mechanisms have been evolved from each other. When such an understanding is possible it will probably provide useful evidence concerning the phylogeny of recent mayflies. It is reasonable to suppose that the feeding apparatus of *C. dipterum* and *B. rhodani* most closely resembles that from which other mechanisms developed, because the orthopteroid appearance of the head and mouthparts in these genera is that which would be expected in the ancestral mayfly stock, and occurs in *Pthartus*, a larva described from the Permian by Handlirsch (1918) that closely resembles a modern baetine larva.

ACKNOWLEDGMENTS

This work was carried out while I held a Department of Scientific and Industrial Research Studentship in the University of Leicester under the supervision of Professor H. P. Moon to whom I am grateful for much stimulating discussion. I am grateful to Dr D. S. Guthrie for his criticism of the text.

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KEY TO THE LETTERING TO FIGURES

A.ar.s	Anterior articulatory surface of mandible.	La	Lacinia.
Ant	Antennal base.	La.ab	Anterior bristles of lacinia.
Ap	Apodeme of posterior wall of postmentum.	La.pb	Posterior bristles of lacinia.
		Lb.eb	Bristles on edge of labrum.
Ba.S	Basal sclerite.	Lb.ih	Hairs on inner surface of labrum.
bl.	Blade of right molar surface.	Lb.n	Median notch in edge of labrum.
Ca.	Cardo.	Lb.p	Labial palp.
Cad	Distal part of cardo.	Lbr.	Labrum.
Ce	Compound eye.	M.Oc	Median ocellus.
Ca. in	Inflected portion of distal part of cardo.	Md.h	Mandibular hairs.
		Md.l	Left mandible.
		Md.r	Right mandible.
Clp	Clypeus.	Mx.	Maxilla.
Cp.p	Posterior wall of head capsule.	Mxp	Maxillary palp.
Cp. cut	Cut edge of head capsule.	O.c	Outer canine.
Cs	Coronal suture.	Oc.l	Left ocellus.
Cap	Proximal part of cardo.	Occ	Occiput.
Eph	Epipharyngeal surface.	Occ.f	Occipital foramen.
Eph.b	Epipharyngeal bristles.	P.ar.s.	Posterior articulatory surface.
Es	Epistomal suture.	pb.	Bristles on the terminal segment of the labial palp.
F	Frons.		
Fs	Frontal suture.	PG.	Post gena.
G	Gena.	Pgl.	Paraglossa.
G.in	Inflected edge of gena.	Pglmb.	Paraglossal bristles.
Gl	Glossa.	Ph	Pharnyx.
HyB	Hypopharynx body.	Pocc.ed	Postoccipital condyles.
Hy.B.db.	Lateral bristles of hypopharynx body.	Pocc.s	Postoccipital suture.
		PoM	Postmentum.
Hy.B.pb.	Proximal bristles of hypopharynx body.	PoM.a.	Posterior arm of postmentum.
		PoOcc.	Postocciput.
I.c	Inner canine of mandible.	PrM.	Prementum.
L.ar.s	Lateral articulatory surface.	Pro	Prosthecа.

Pro.c	Preoral cavity.
r	Ridge at distal end of anterior tentorial arm.
SL	Superlingua.
SL.h	Fine bristles on tips of superlinguae.
SL.th	Thickened edge of superlingua.
Sog	Suboesophageal ganglion.
St	Stipes.
t	Tendon of dorsal adductor muscle (6) of mandible.
TA	Anterior arm of tentorium.
TB	Body " "
TD	Dorsal arms " "
TP	Posterior " "
Tor	Torma.
V.	Vertex.

KEY TO THE NUMBERS USED TO DENOTE MUSCLES IN THE FIGURES AND TEXT

1. Labrum retractor.
2. Labrum protractor.
3. Cranial abductor of mandible.
4. Tentorial abductor of mandible.
5. Tentorial adductors of mandible.
6. Dorsal adductors of mandible.
7. Hypopharyngeal-mandibular.
8. Stipes adductor.
9. Cardo adductor.
10. Cardinal-cranial.
11. Cranial-lacinial.
12. Stipital-lacinial.
13. Adductor of 1st segment of maxillary palp.
14. Abductor of 1st segment of maxillary palp.
15. Adductor of 2nd segment of maxillary palp.
16. Abductor of 2nd segment of maxillary pulp.
17. Posterior retractor of prementum.
18. Anterior " " "
19. Dorsal posterior retractor of hypopharynx.
20. Ventral posterior retractor of hypopharynx.
21. Extensor of paraglossa.
22. Protractor of glossa.
23. Abductor of 2nd segment of labial palp.
24. Abductor of 1st segment of labial palp.
25. Adductor of 2nd " " " "
26. Adductor of 3rd " " " "
27. Protractor of the prementum.
28. Dorsal retractor of hypopharynx.

THE WEIGHTS OF WILD HOUSE MICE (*MUS MUSCULUS* L.) LIVING IN CONFINED COLONIES

BY

PETER CROWCROFT

Zoology Department, British Museum (Natural History)

AND

F. P. ROWE

Infestation Control Division, Ministry of Agriculture, Fisheries & Food, Hook Rise, Tolworth, Surbiton, Surrey.

[Accepted 10th May, 1960]

(With 2 figures in the text)

Wild house mice supplied with excess food and confined in pens rapidly became grossly overcrowded. The mean body weights at specified ages of mice born when overcrowding was acute have been compared with those of mice born earlier, in order to test the hypothesis that overcrowding depresses body weight. In three of the four pens studied the more crowded animals were lighter, but in the fourth they were heavier. There is evidence of great inherent variability in body weight in the species.

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INTRODUCTION

Scheffer (1956) reviewed the limited information available about the effects of overcrowding on the growth and weight of wild mammals. When dealing with the house-mouse (*Mus musculus* L.), he tentatively concluded that overcrowding causes a decrease in mean weight, basing this entirely on the work of Crew & Mirskaia (1931), who confined adult laboratory mice in small cages at various "population densities". He appeared reluctant to accept the conclusion of Strecker & Emlen (1953), who worked with confined colonies of wild house mice with a limited food supply, that the effect of overcrowding was an increase in the mean body weight of the survivors.

There is no doubt that the mean weight of mice confined in large pens or cages does increase when overcrowding becomes acute, the increase being caused by changes in the age-structure of the populations. Colonies studied by Southwick (1955) and Christian (1956) showed heavy mortality among the young and reduced fecundity among the females as consequences of over-

crowding. Strecker & Emlen (loc. cit) and Crowcroft & Rowe (1957) found relatively little infant and juvenile mortality, and greater reduction in female fecundity, but the effects on the age-structure of the populations were similar.

These studies supply virtually no information about the effect of overcrowding on the weights of individuals. The pioneer work of Crew & Mirskaia (loc. cit) on reproduction is scarcely relevant to this problem, as their artificial aggregations of adult mice confined in small cages cannot be regarded as " populations " with specific " population densities ", especially as the numbers were maintained by adding fresh adults as fast as they were killed off by fighting.

Some information is available about the weights of wild house mice in several habitats (Laurie 1946), and in the case of corn-ricks an approximate measure of population density is also available (Southwick 1958). But the mice examined in these studies have been of unknown age and their weights have little value for comparative purposes, for the weights of sexually mature wild house mice vary from less than 12 g to more than 25 g.

As we had age and weight records for mice living in colonies which became grossly overcrowded, we examined the data for evidence of an effect on weight, acting independently of age or food supply.

MATERIALS AND METHODS

Each colony was founded with one adult male and two adult females. All mice were individually marked, usually before weaning, by clipping the terminal phalanges from combinations of toes of the back feet. The animals were weighed at censuses conducted fortnightly at first and later monthly.

The pens were six feet square, with smooth metal walls two feet high resting on a concrete floor covered with wood sawdust. Eight nest-covers one foot square were provided in each pen. Water, whole wheat and oats, and " Diet 41 " (Bruce & Parkes 1949) were given in excess at numerous points and replenished weekly. Hay was scattered about to provide nesting material and to supplement the diet.

Each of the four colonies dealt with here (pens A, B, C, and D) reached approximately 130 mice over the period covered by the analysis.

There are insufficient data for making direct comparisons between mice of the same age living under different conditions of crowding in the same pen. Also it is pointless in our present state of knowledge to compare the mean weights of given age classes at specified " population densities ", for the degree of overcrowding, from the mouse's point of view, may be related less to the number of animals per unit area, than to the social organisation of the colony. This is, in turn, largely determined by the amount and arrangement of the " cover ", which cannot be measured at present.

The method adopted, therefore, was to take a series of animals born early in the growth of each of the four colonies and compare their mean weights at specified ages with those of a series born later in the same pen. Thus the figures from which the mean weight for an age-class has been calculated were not all obtained at the same census, and the animals in any one age-class entered it at slightly different times (except in the case of litter-mates) and possibly under different social conditions. It is certain, however, that all of the individuals

making up a late-litter group were confined with more mice than those of the corresponding early-litter group. If overcrowding has a progressively depressing effect on body weight, the mean weights of the late-litter groups should be lower.

Males have been used for the analysis because of the effects of breeding on the weights of females. In pen B, however, in which a large proportion of the females never bred (prior to experimental dispersal) sufficient figures are available for making a comparison between the sexes.

THE GROWTH CURVE

Robertson (1916) showed that uncrowded laboratory mice continued to increase in weight throughout life, but there is no information at all available about the growth of either free-living or captive wild house mice. In Fig. 1, therefore, we have given the age/weight data of 63 male mice born in pen B. This shows wide variation in weight at all ages, but on the average, weight continues to increase at least up to 400 days, and a curve drawn through the means is similar to that obtained by Robertson. The data for the males in the other three pens, and for the females in pen B, give growth curves of similar form.

INDIVIDUAL VARIATION

There is wide variation in weight among males of comparable age in all four pens (Table 1). When the means are examined, it is clear that the females in pen B are significantly lighter than the males, (Table 2) and that there are marked differences between the mean weights of males from different pens (Table 3).

Table 1—Variation in body weight among male house mice of similar age in four pens.

Age-class (days)	Weight range in grams.				Maximum difference within the class	Number of observations
	Pen A	Pen B	Pen C	Pen D		
20–39	5·7–14·1	5·1–14·7	3·7–11·0	3·8–12·2	11·0	250
40–59	10·4–16·7	8·4–16·4	10·5–15·6	8·5–17·3	8·9	217
60–79	10·0–18·8	9·8–17·0	10·0–16·6	10·3–16·5	9·0	220
80–99	10·7–20·3	11·7–17·3	10·8–17·1	11·1–20·0	9·6	235
100–119	12·3–20·8	12·1–17·8	11·8–19·2	11·8–18·0	9·0	225
120–139	12·2–22·8	12·7–18·5	12·1–18·4	12·3–21·0	10·7	210
140–159	11·8–24·2	14·3–19·0	12·0–21·6	12·8–20·9	12·4	214
160–179	12·2–25·1	14·1–19·9	13·1–20·6	14·5–20·9	12·9	213
180–199	14·8–25·4	14·7–20·1	13·5–23·2	14·2–21·5	11·9	187
200–239	13·5–28·4	15·1–22·8	14·5–22·1	15·5–22·1	14·9	240
240–279	—	16·3–22·1	15·6–21·7	16·2–23·9	8·3	211
280–319	—	17·0–23·6	—	—	6·6	66

The wide variation within age-classes is not explicable in terms of differences in social status. The few males capable of maintaining territories under the experimental conditions were at times, but not always, the heaviest for their

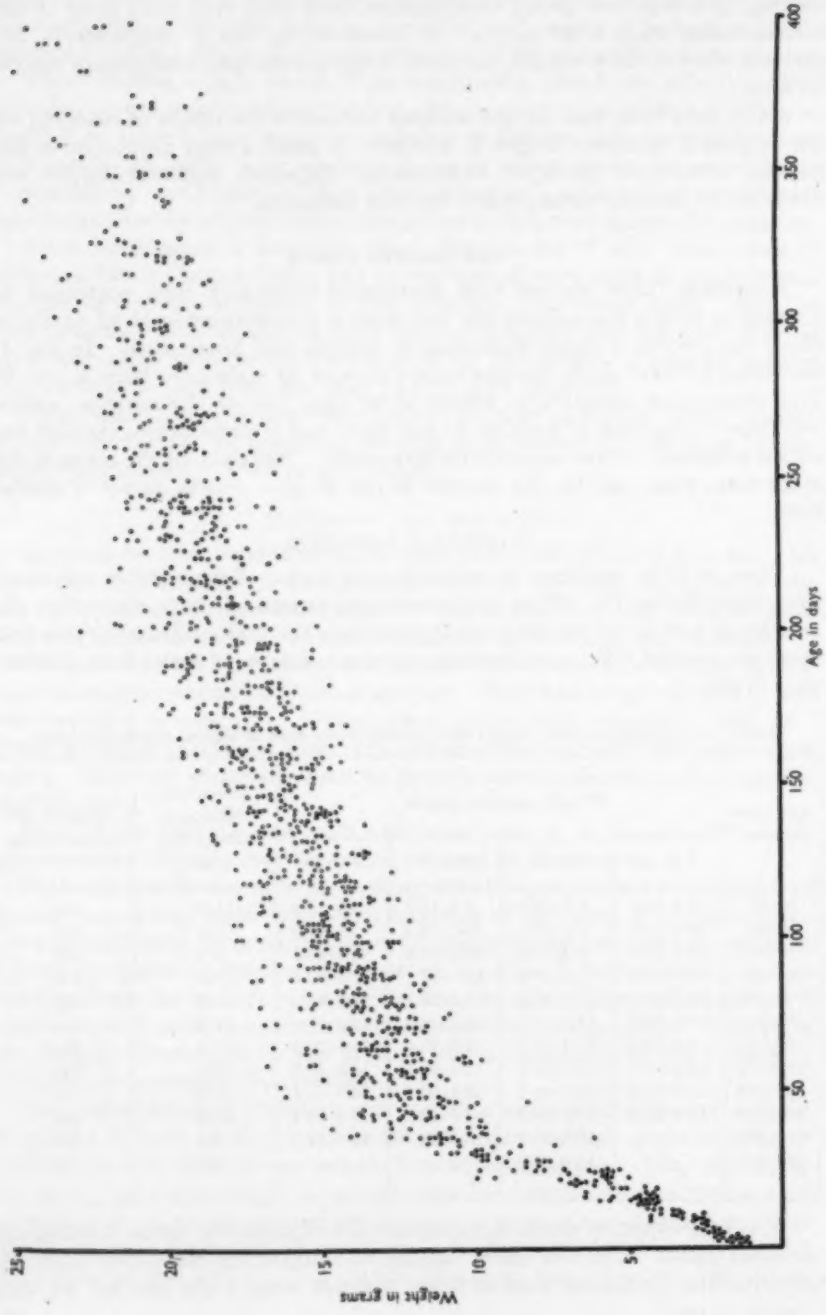

Fig. 1—Age/weight data of wild house mice living in a confined colony (pen B).

age, and the adoption of a territory sometimes led to a fall in weight, probably because of the increased activity.

Sudden changes in status, such as befell some males which became social outcasts, were often accompanied by a fall in weight, but not to a point below the minimum for the age-class. The majority of males were not involved in fighting, and among these "neutral" individuals were to be found both the heaviest and the lightest individuals with respect to age.

Table 2—The mean body weights of early- and late-litter male and female house mice born in one colony (pen B).

Age-class (days)	Early-litters		Late-litters		Difference between means	
	Male	Female	Male	Female	Male	Female
20–39	9·20	8·96	8·73	8·12	− 0·47	− 0·84
40–59	12·95	11·14	11·95	10·51	− 1·00*	− 0·63
60–79	13·97	12·12	12·46	11·75	− 1·51*	− 0·37
80–99	14·48	12·58	13·75	12·73	− 0·73*	+ 0·15
100–119	14·90	13·20	14·82	13·20	− 0·08	0·00
120–139	15·97	13·18	15·48	13·76	− 0·49	+ 0·58
140–159	16·38	13·67	16·20	14·28	− 0·18	+ 0·51
160–179	17·37	14·06	16·83	14·96	− 0·54	+ 0·90*
180–199	17·62	14·17	17·83	15·63	+ 0·21	+ 1·46*
200–239	18·83	14·68	18·66	15·90	− 0·17	+ 1·22*
240–279	19·56	15·46	19·48	16·35	− 0·08	+ 0·89*
280–319	20·41	16·58	20·23	16·56	− 0·18	− 0·02

*=statistically significant at least at the 5 per cent level.

Table 3—The mean body weights of early- and late-litter male house mice born in three colonies (pens A, C and D).

Age-class (days)	Pen A			Pen C			Pen D		
	Early-	Late-	Difference	Early-	Late-	Difference	Early-	Late-	Difference
20–39	8·35	8·81	+ 0·46	7·51	7·74	+ 0·23	8·65	7·65	− 1·00
40–59	14·06	12·32	− 1·74*	12·31	12·37	+ 0·06	14·31	10·76	− 3·55*
60–79	15·48	14·10	− 1·38*	12·34	13·69	+ 1·35*	14·89	12·40	− 2·49*
80–99	15·85	14·80	− 1·05	13·56	14·51	+ 0·95*	15·98	12·93	− 3·05*
100–119	17·75	16·11	− 1·64*	14·03	16·59	+ 2·56*	16·37	13·87	− 2·50*
120–139	17·90	16·33	− 1·57*	14·75	16·77	+ 2·02*	17·17	14·61	− 2·56*
140–159	19·34	16·55	− 2·79*	15·32	17·70	+ 2·38*	17·74	15·83	− 1·91*
160–179	19·36	17·33	− 2·03*	15·73	17·76	+ 2·03*	18·05	16·83	− 1·22*
180–199	19·96	17·73	− 2·23*	16·43	17·96	+ 1·53*	18·55	16·96	− 1·59*
200–239	20·71	17·89	− 2·82*	17·07	18·02	+ 0·95	18·80	18·51	− 0·29
240–279	—	—	—	18·13	18·62	+ 0·49	19·60	18·91	− 0·69

*=statistically significant at least at the 5 per cent level.

The growth curves of five males (Fig. 2) illustrates the kind of variation observed. The two unbroken lines represent two "neutral" males from pen A. The lower shows the sharp fall in the growth rate commonly observed

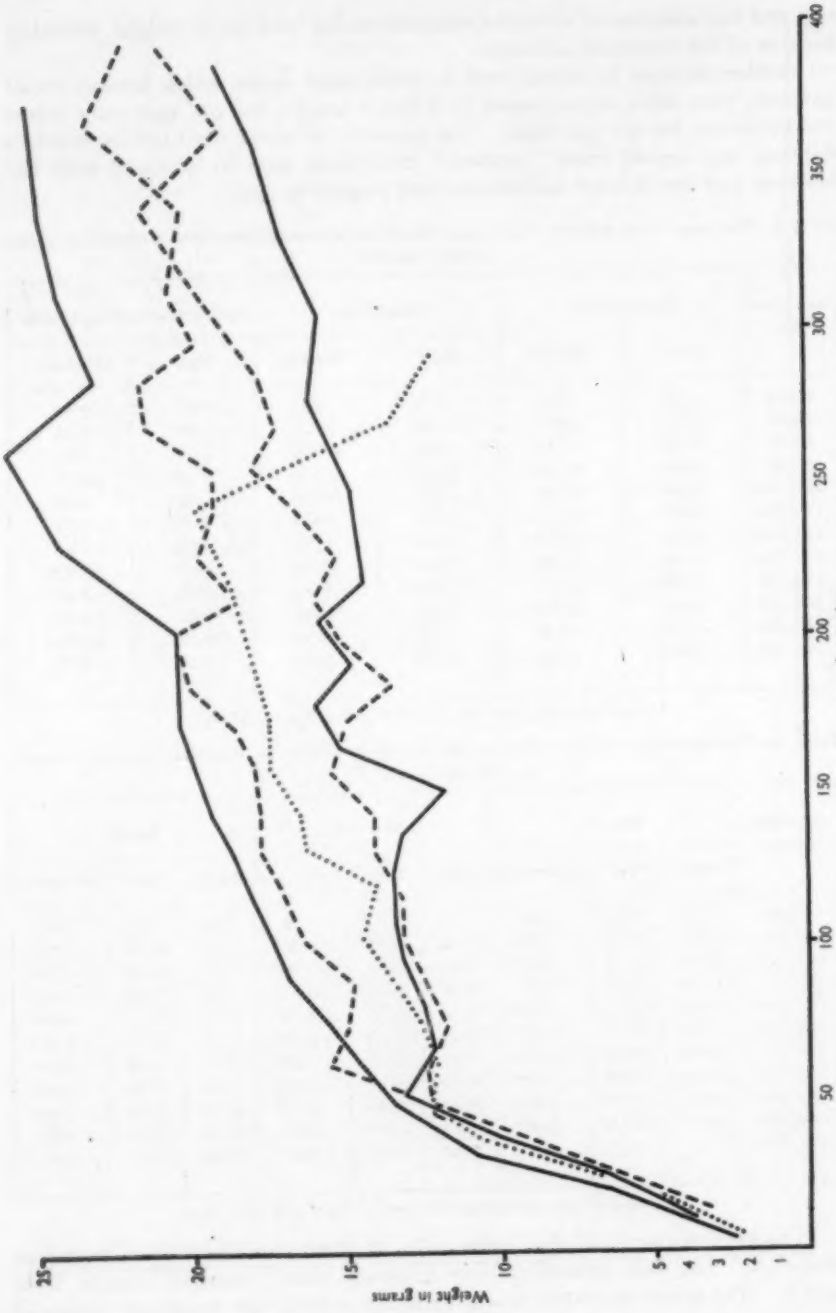

Fig. 2—The growth of five male house mice from confined colonies, showing typical variation. For details see text.

when young males are leaving the protective cover of females and infants, but the upper does not, although this animal was also growing under crowded conditions. The two broken lines show the growth of two males from pen C. One (lower line) remained a " neutral " while the other became a dominant between the ages of 184 and 201 days. The establishment and maintenance of a territory led to a fall in weight followed by a slower rate of increase. Subsequently this dominant was deposed and wounded, but the attendant fall in weight was insignificant. The dotted line represents a " neutral " animal from pen B. When examined at 242 days of age this animal was in good condition, but a month later it was clearly sick (not bitten), and it died before the next census. The last two weights, and those from similar cases have been excluded from the calculations of the means.

EARLY-LITTERS AND LATE-LITTERS COMPARED

Figure 1 combines the data from the first 31 males and the last 32 males born in pen B. The mean weights of the two series at specified ages are given in Table 2. Those born later, and growing under more crowded conditions are in general lighter in weight. Although the difference is statistically significant only during the period 40–100 days of age, further statistical treatment would probably reveal a significant trend throughout.

The late-litter males in pens A and D are also lighter in weight and the difference is significant at most ages. But in pen C, the late-litter males are significantly heavier (Table 3). When the early- and late-litter females in pen B are similarly compared (Table 2), the differences are negligible, except during the age range 160–280 days, when the late-litter animals are significantly heavier.

DISCUSSION

Three out of four colonies studied showed lower mean body weights in the late-litter males of almost all age-classes. It is certain that the males were more active at higher population densities and their lighter weights may have been due to this. Pen B is of particular interest, for this colony had a stable social structure and negligible adult mortality, probably due to the rapid attainment of high numbers prior to the development of agressive behaviour among the males. The age at which the late-litter males in this pen were significantly lighter (40–99 days) corresponded with the period during which they had to make the drastic social change from association with mothers and young in nest boxes subject to little disturbance, to association with other males or to the establishment of individual territories.

The fourth colony, in pen C, showed the late-litter males to be significantly heavier than those born earlier, and prevents us from drawing any general conclusion relevant to Scheffer's hypothesis. It might be argued that this exceptional result was due to genetic factors, but if so, genetic factors must also be considered as possible causes for the lighter weights of the late litter males in pens A, B and D.

The heavier weights of the late-litter females in pen B were found to be due to the accumulation of excessive fat associated with prolonged anoestrus

(see Strecker & Emlen, 1953; Crowcroft & Rowe, 1958). This weight difference disappeared after the age of 280 days simply because the early-litter females also entered anoestrus when overcrowding became acute. Judging by the poor breeding records of the females, some crowding effects began to operate as soon as the first litters of the two original females were prevented from dispersing. This raises the possibility that physiological effects of overcrowding on body weight also may have been operating, indeed may have been maximal, before the late-litter mice were born.

A comparison between groups of mice of known age living under differing, but in general much lower levels of overcrowding than those experienced in our pens, might yield conclusive evidence of an adverse effect of overcrowding on body weight independent of food supply, but the practical difficulties of obtaining sufficient data appear to be insurmountable.

The most interesting result of the present analysis is the evidence of great variation in body weight among mice of comparable age living under comparable physical and social conditions. There is undoubtedly a correlation between social dominance and high body weight, but the former appears to be a consequence and not a cause of the latter. Great disparity in body weight is found between animals of apparently similar social status, and for the present it must be ascribed to differences in genetic constitution. In the age-class 20–39 days the wide variation (Table 1) may be accounted for by age disparity within the class, as this is a period of very rapid growth. When mice are 200 days old however, growth is relatively slow yet within the age-class 200–239 days some apparently healthy males weigh only half as much as others. Viewed from the other aspect, this wide variability means that mice six weeks old and mice six months old may have the same body weights. The differences between the mean body weights of males from different wild-caught parents (Table 1) provide additional evidence of considerable inherent variability in body weight in this species.

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THE FOOD OF THE PINE MARTEN *MARTES MARTES* IN WEST ROSS-SHIRE, SCOTLAND

BY

J. D. LOCKIE

Nature Conservancy, 12 Hope Terrace, Edinburgh 9

[Accepted 14th June, 1960]

(With 1 figure in the text)

This paper concerns the food of the pine marten *Martes martes* in the Beinn Eighe National Nature Reserve, West Ross-shire, between 1956 and 1958. The technique of studying food from droppings and the need for correction factors are discussed. The study is based on 337 droppings.

The food eaten was varied both in size and nature but small rodents and small birds formed the bulk of the food at all times of the year. Coleoptera, Lepidoptera, carrion, fish and berries were eaten seasonally. Small prey appeared to be preferred. Ninety per cent of the small rodents eaten were short-tailed voles *Microtus agrestis* despite the fact that bank voles *Clethrionomys glareolus* and woodmice *Apodemus sylvaticus* were probably more abundant and the martens' activity rhythm brought them into contact with all three species.

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INTRODUCTION

This is an account of a study of the food of pine marten between March 1956 and February 1958 in and about a remnant of pine and birch forest on the Beinn Eighe National Nature Reserve in West Ross-shire. The wood covers about 500 acres and consists of small areas with dense mature stands of pine (*Pinus sylvestris*), more extensive areas with well-spaced trees a result of wartime felling, and a birch wood (*Betula pubescens*) with flush grassland above. Undercover in the pine wood is mainly tall heather (*Calluna vulgaris*) and a thick mat of *Sphagnum* spp. Rowan (*Sorbus aucuparia*) is common. In the birch wood the undercover is blaeberry (*Vaccinium vitis-idaea*) with here and there patches of the grasses *Molinia caerulea*, *Deschampsia caespitosa*, and *D. flexuosa*. Marten are not restricted to the wood but the resident animals are thought to spend much of their time there judging from the distribution of droppings and a small number of sight records in and around the wood.

TECHNIQUES OF STUDY

To avoid interfering with the population of marten the food studies have depended upon the analysis of droppings collected at 2-monthly intervals. The identification of the droppings gave little difficulty in the study area since stoats (*Mustela erminea*), with whose faeces those of marten can be confused, are absent. Experience was gained by noting the characteristics of those droppings which contained marten hair and by collecting weasel (*Mustela nivalis*), stoat and fox (*Vulpes vulpes*) droppings from elsewhere for comparison. Since all droppings were cleared from a standard route at each collection, their age was known to within two months. But, in order to allocate droppings collected elsewhere than on the standard route to a 2-month period, samples were left to weather between collections and their appearance used as a guide.

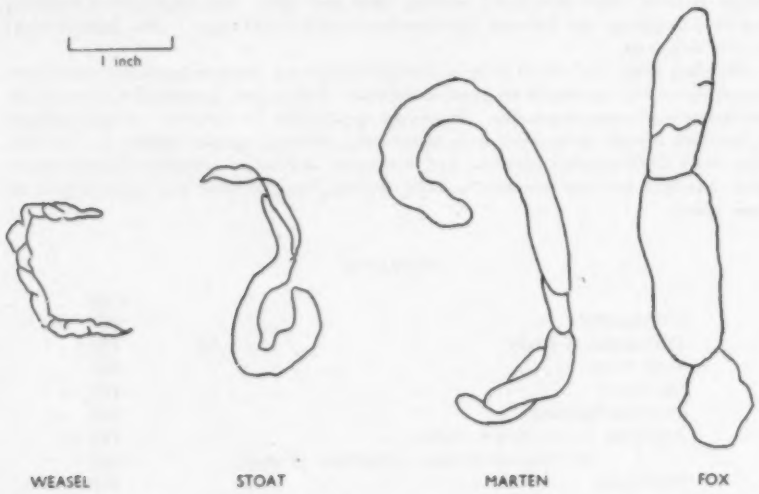

Fig. 1—Typical droppings of three mustelids and fox.

The identification of prey remains in droppings was aided by a reference collection which included the bones, fur or feathers, etc., of the main potential prey species in and around the study area. There is no indication that any major foods have been missed, for all foods, even the larvae of lepidoptera, were identifiable in the droppings.

The processing of each dropping consisted of (1) thorough washing in a sieve, (2) identification of the various prey remains, (3) the estimation of the relative proportion of the prey remains, and (4) drying and weighing. From this the weight of dry undigested matter from each prey could be calculated. I have called this method " weight of undigested matter ". Next, factors (see later) were applied to the data to correct any bias due to differential ingestion and digestion. From these corrected figures the relative proportion of the various prey species in the diet was obtained (Table 1).

This rather elaborate procedure was developed after it was found in feeding tests with foxes that the analysis of data by " occurrence " was variable in its accuracy whereas that by " weight of undigested matter " was much more consistent (Lockie, 1959).

One difficulty of the method of " weight of dry matter " is that the relative proportion of prey remains depends on a subjective estimate. In the present study, seven checks were therefore made in which selected remains (vole, Coleoptera and Lepidoptera larvae) were removed and weighed and their true value compared with that estimated previously. The errors in the estimate ranged from —1 per cent to +6 per cent.

A correction factor is the weight of the prey item eaten divided by the dry weight of undigested matter of this prey in the droppings and can be discovered by feeding tests. No feeding tests have been made with marten but, in this instance, it is possible to dispense with them because equivalent tests have been done with foxes. An examination of the remains of small rodents, large rodents and small and large birds in the droppings of marten, show that marten eat these foods in a similar manner to the foxes on which feeding tests were done (Lockie *ibid.*). For example, both marten and fox ate small rodents completely. The proportion of marten droppings containing small rodent which also contained rodent teeth was 57 per cent ; the comparable figure in the tests with foxes was 50 per cent. Likewise both marten and fox usually discarded only the primaries and tail feathers of small birds and sheared through the primaries of large birds near the base of the quills. The feet and mandibles of small birds occurred in both fox and marten faeces. I therefore feel justified in using for the marten the correction factors established for the fox for the following prey groups : rabbit, large and small bird, and small rodent. Correction factors, for prey groups not tested with foxes, were calculated in the following manner. Known numbers of Coleoptera, lepidopterous larvae and cocoons, and wild fruit were obtained from selected marten droppings. The dry weight of these food remnants was then related to the weight of similar live animals and fresh fruit collected in the field. The correction factor for birds' eggs is the weight of a complete egg divided by the dry weight of shell and membrane. The correction factor for deer, sheep and fish has been arbitraily fixed at that of " large bird " and is probably too low, but since these items were not eaten much, the error is not serious. Correction factors for marten food are listed in Appendix 1.

Another possible error in assessing the relative importance of different foods arises from the fact that a predator may not eat large prey completely nor return later to finish it off. This error is unlikely to be important in the present study since the prey of these marten is mostly small and can be consumed at a sitting. No correction for this has therefore been attempted.

THE FOOD EATEN

The food eaten was varied both in its nature (berries and flesh) and in the size of the individual items which ranged from the beetle *Carabus violaceus* to large birds such as woodpigeons (*Columba palumbus*) (Table 1).

Small rodents occupied a considerable part of the diet at all seasons and were in both years supplemented by small birds, insectivores, insects and carrion. Other foods, notably young rabbits (*Oryctolagus cuniculus*) or hares (*Lepus timidus*), Lepidoptera and berries, were eaten in large quantities as they became available.

Table 1—Seasonal and annual changes in the food of pine marten.

Prey	Percentage estimated weight (corrected)					
	1956–57			1957–58		
	Mar.–Jun.	Jly.–Oct.	Nov.–Feb.	Mar.–Jun.	Jly.–Oct.	Nov.–Feb.
Small rodent	64	28	81	45	69	75
Small bird	7	2	18	3	12	17
Large bird	1	4	—	0·5	—	—
Insectivora	5	4	—	—	3	3
Rabbit or hare	2	T	—	33	—	—
Lepidoptera	19·5	—	—	0·5	—	—
Coleoptera + Hymenoptera	0·5	2	—	0·5	2	0·5
Fish	—	T	—	3	T	0·5
Carrion	—	4	—	13	2	3
Berries	—	56	—	—	12	—
Grass	—	T	1	1	—	0·5
Eggshells	1	—	—	0·5	—	0·5
Total	100	100	100	100	100	100
No. of samples	91	95	15	56	51	29
Wt. (grams) of undigested matter (uncorrected)	130	113	13	84	61	39

Small rodents

The three important small rodents in the area are identifiable in the faeces by their teeth, Morrison-Scott (1952). It has been shown (Lockie, 1959) that the relative proportions of the total number of molar teeth of the short-tailed vole (*Microtus agrestis*), bank vole (*Clethrionomys glareolus*), and wood mouse (*Apodemus sylvaticus*) recovered from faeces is a good measure of the proportions in which these rodents were eaten.

In order to compare the proportions of the three rodent species eaten by marten with the proportions of these foods occurring in the habitats frequented by marten, trapping was done. Five trap-lines were placed in the main habitats, each line consisting of ten points ten yards apart. Four traps were placed at each point, two baited Longworth traps and two baited breakback traps. So far as was possible breakback traps were placed where *Microtus* would be likely to run, in an attempt to offset the attraction that Longworth's have for *Apodemus* and *Clethrionomys*.

The general impression obtained from trapping and by searching for runs during 1957 and 1958 was that *Microtus* was distributed through the wood in small more or less isolated pockets and was no more abundant outside the wood than in suitable areas inside. Further, even allowing for the fact that *Apodemus* and *Clethrionomys* were probably more easily trapped than *Microtus*, the first two species were more abundant than *Microtus* as indeed one would expect them to be. Nevertheless, the proportion that *Microtus* represented in the small rodent prey of marten was consistently high (over 90 per cent) and the proportion of *Microtus* in the traps consistently low (0–12 per cent) (Table 2). The inference is that there was an overwhelming selection of *Microtus* by pine marten.

Table 2—Percentage proportion of small rodents in marten and in traps (1956–58).

Period	Source	*Microtus*	Percentage of *Clethrionomys*	*Apodemus*	No. of rodent teeth (marten) or rodents (traps)
March–June	Marten	94	4	2	192
	Traps	0	32	68	34
July–October	Marten	93	5	2	88
	Traps	—	—	—	—
November–February	Marten	92	7	1	48
	Traps	12	39	49	37

Marten have been seen both by day and after dark. Of thirteen sight records of marten by various observers in and around the study area, five were after dark, three at dusk and five by day. Two of the records at dusk were of an animal that appeared from its sleeping place one hour before dark on consecutive nights and apparently set off hunting. It would seem that the activity rhythm, so far as it is known, brings the marten into contact with all three rodents.

Probably marten, like foxes, have specialized methods of hunting for *Microtus*. *Apodemus* and, to a lesser extent, *Clethrionomys* are usually too difficult to catch presumably because both live in a burrow as opposed to a run system and both, especially *Apodemus*, are extremely agile.

Neither Cowan & MacKay (1950) in the Canadian Rockies nor Lensink *et al.* (1955) in Alaska found that marten took more *Microtus* spp. than *Clethrionomys* spp. where both were present. Both studies do, however, show that very few *Peromyscus*, the habits of which are similar to those of *Apodemus* in Britain, were taken by marten.

Birds

Avian prey has been grouped into large and small, small birds being those up to the size of a blackbird (*Turdus merula*).

The most abundant birds available in and around the study area include blue tit (*Parus caeruleus*), great tit (*P. major*), coal tit (*P. ater*), long-tailed tit (*Aegithalos caudatus*), wren (*T. troglodytes*), treecreeper (*Certhia familiaris*), robin (*Erithacus rubecula*), blackbird, meadow pipit (*Anthus pratensis*), crossbill (*Loxia curvirostra*), woodcock (*Scolopax rusticola*), woodpigeon, hooded crow (*Corvus corone*), fieldfare (*Turdus pilaris*) in winter, chaffinch (*Fringilla coelebs*), red grouse (*Lagopus scoticus*) (uncommon), mallard (*Anas platyrhynchos*), and domestic fowls at nearby farms.

Although the prey could usually be grouped according to size without difficulty, the identification of species was much less easy and only 30 per cent of prey items could be identified with reasonable certainty. These were : blue tits (4 times) ; unidentified tits (3) ; wrens (3) ; pipits and chaffinches (2 each); one each of robin, blackbird and treecreeper ; woodpigeons (2) ; adult grouse (2) ; and young grouse (1). Twenty-six small and three large birds were unidentified.

The marten caught small birds rarely caught by other predators namely, blue tits (including unidentified tits) and wrens. A sparrowhawk (*Accipiter nisus*) nesting in the study area in 1957 brought only chaffinches to the nest and was seen once to kill a blackbird. Likewise in Holland, Tinbergen (1946) found that wrens occupied 0·06 per cent of the sparrowhawk's prey and blue tits 4·5 per cent. In tawny owls (*Strix aluco*) near Oxford, tits occupied only 11 per cent of the identifiable avian food and no wrens were identified (Southern, 1954). In contrast, more than half the identified avian prey of marten consisted of tits and wrens.

Contrary to expectation the marten took small birds most frequently in winter, and not in summer when many fledglings are available. The fledgling of an unidentified small bird was detected once in the droppings. Possibly some nestlings were eaten but little of these would survive in the faeces and so would be missed during analysis. Eggshells appeared in the droppings occasionally (5 occurrences out of 556 prey occurrences). All appeared to be of large birds, possibly woodpigeon and duck.

Insectivores

Insectivores (shrews *Sorex* spp. and occasionally moles *Talpa europaea*), occurred in smaller numbers than their abundance in the habitat suggested they should. This agrees with previous work on the food of mammals to whom insectivores appear distasteful.

Rabbit and Hare

Both rabbits and mountain hares were rather uncommon during this study and most occurrences probably refer to young mountain hares.

Insecta

Coleoptera appeared regularly in droppings but formed a small part of the total diet. The species most frequently found were *Carabus violaceus*, *Geotrupes stercorarius* and *Feronia* spp. In contrast, large numbers of pupae and larvae of the oak eggar moth (*Lasiocampa quercus*) were eaten seasonally

and during April 1956 many droppings contained the remains of up to thirty pupae or larvae. In this habitat, larvae of the oak eggar eat heather and pupate on it.

Hymenoptera identified in droppings were bees (*Bombus* spp.) and wasps (*Vespa* spp.). Wasps' nests were occasionally dug out ; larvae were identified in only one dropping.

Fruit

Both blaeberries and rowan berries were eaten in large quantities : rose-hips (*Rosa* spp.) occurred occasionally in the droppings.

Various

Fish remains appeared in the droppings from time to time and the gill raker of a sea trout (*Salmo trutta*) or salmon (*Salmo salar*) was found in a nest box used by marten for sleeping. Most of the fish were probably trout found dead or scooped from the shallows of hill streams.

Carrion, mainly red deer (*Cervus elaphus*) was eaten in small amounts throughout the year and in the winter of 1957–58 strips of deer carrion were hoarded by marten in a hole in a birch tree, fifteen feet from the ground.

Grass was found in small quantities in some droppings and probably was ingested with the prey. During early spring and winter, however, some droppings contained only grass.

In view of the readiness with which marten dig up wasps' nests, it might be expected that they would also scratch or dig for earthworms (Lumbricidae). In fact, only 6 per cent of 358 droppings showed any sign of earthworm chaetae. In at least 50 per cent of these the earthworm remains could have come from prey associated in the same sample, e.g. small birds, shrews and woodmice. There is little indication that the marten deliberately tried to catch earthworms.

Although frogs were abundant in summer, no trace of them was found in the marten droppings examined. Remembering the fact that even caterpillars can be identified from droppings, it seems unlikely that all trace of frogs disappeared in digestion. The inference is that frogs, despite their abundance, were not eaten. There are, in fact, few references in the literature to marten eating frogs and then only when other food is scarce (Schmidt, 1943).

DISCUSSION

The marten on the Beinn Eighe Nature Reserve eat a great variety of animal and vegetable food. At all times of year, however, small rodents, particularly *Microtus agrestis*, form an important part of the diet. Small birds are the second most important prey and a variety of other prey is taken seasonally, sometimes in large quantities. In other investigations (summarized in Lensink *et al.* 1955 ; Quick, 1955) microtine rodents were the basic prey of marten and sable (*Martes zibellina*), in the Canadian Rockies, the Shantar Islands, the Sajan Mountains of Siberia, Kamchatka, the Ural Mountains and Central Alaska. Studies in Washington and Montana demonstrated that squirrels (Sciuridae) were an important food but Jurgenson (1954) showed that there is great variation in the extent to which squirrels are important in the diet of marten in various parts of Russia and this is evidently

not explainable only by cycles of squirrel population. In captivity marten will eat practically anything (Remington, 1952).

The picture is of a carnivore with a very wide range of acceptable foods and with hunting techniques and activity rhythm that make a wide range available. The ease with which marten turn to seasonally abundant foods of great variety is shown in this study and has previously been noted by Quick (1955) in Northern British Columbia. This suggests that marten are primarily guided in their choice of foods by the availability of the various prey species. But availability is often complex, depending not only on numbers of prey but also on their habits in particular habitats. Even so, it is perhaps surprising that this active and versatile predator should find *Microtus* so very much more available than *Clethrionomys* and *Apodemus*.

ACKNOWLEDGMENTS

I am grateful to the Warden of the Beinn Eighe Nature Reserve, Mr J. Polson, B.E.M., for much assistance in discussion and in the field, and to W. J. Eggeling and H. N. Southern for helpful comments.

APPENDIX 1

Correction factors

Group	Factor	Source
Small mammal	22	Lockie (1959)
Rabbit and hare	43	,, ,,
Large bird	61	,, ,,
Small bird	37	,, ,,
Coleoptera	5	21 from marten droppings : 20 fresh
Lepidoptera : larvae and cocoons	12	30 from marten droppings : 10 fresh
Eggshells	15	1 woodpigeon : 1 hen
Fish, Deer, Sheep	61	arbitrarily fixed as large bird
Berries	14	134 from marten droppings : 150 fresh

APPENDIX 2

Food of marten (occurrence of prey)

	No. of occurrences of principal prey					
	1956–57			1957–58		
	Mar.–Jun.	Jly–Oct.	Nov.–Feb.	Mar.–Jun.	Jly–Oct.	Nov.–Feb.
Small rodent	66	33	12	39	28	21
Small bird	15	5	2	4	10	7
Insecta (Lepidoptera)	45	—	—	8	—	—
Insecta (other)	19	31	2	8	15	4
Fruit	—	81	—	—	22	—
Various	11	15	3	21	4	15
Total	156	165	19	80	79	47

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THE MECHANISM OF WAVE RIDING IN PORPOISES

BY

K. M. BACKHOUSE AND P. J. G. SMART

Charing Cross Hospital Medical School, London, W.C. 2

[Accepted 14th June, 1960]

(With 1 plate and 1 figure in the text)

The characteristics of wave riding porpoises are described showing that the animals use a breaking bow wave in much the same way as a human surf-rider planes in a breaking wave.

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INTRODUCTION

Problems of wave riding in dolphins and porpoises appear to have taken on rather a major significance since Woodcock (1948) put forward what has become accepted as the first scientific description of the phenomenon. His later paper with McBride (1951), making theoretical suggestions as to the mechanism, however, completely neglected the characteristics of the bow wave in which he described the phenomenon. Hayes (1953) likewise theorises on a simple wave form rather than a bow wave, which weakens his otherwise excellent hydrodynamic interpretation. Scholander (1959) took the more practical view of examining the behaviour of hydrofoils in the bow wave of a ship. Hayes's (1959) criticism, on purely theoretical grounds, of Scholander's ideas are unacceptable, as the bow wave of a ship is not the simple hydrodynamic system that Hayes himself describes. Scholander is thus the only author to treat the ridden wave as a bow wave, and he fails to convince in his description only because he pays too little attention to the characteristics of this wave, and does not describe an animal in action.

OBSERVATIONS

We observed sustained wave riding by the common porpoise (*Phocaena phocaena*) on two occasions in the English Channel. The ships concerned were travelling at over 20 knots and each animal was close to the bow in the breaking water. On the first occasion several animals were playing around the bow of an aircraft carrier, and one was lying at the surface with its tail extended in the breaking part of the bow wave. This animal was observed for about a minute before it rolled away from the bow and out of the wave.

The second occasion was from a destroyer cruising at a little over 20 knots, and once again an animal was seen close to the bow in breaking water. For a few seconds at a time it would swing over on to its side and once came out of

the wave. However, a few strokes of its tail got it back into position again where it remained for a further half-minute or so before shearing off in the same way as had the other animal.

Fig. 1—Diagram illustrating wave riding porpoise.

The essential features of both these cases were the same. The porpoise was close into the bow of the ship in the breaking bow wave : the tail was in the breaking part of the water whilst the forepart of the body was at the surface ahead of the crest. The trunk and tail were extended so that the underside of the fluke was presented to the advancing water in the breaking wave. The flippers appeared to be directed rather more lateralwards than is commonly seen in the swimming porpoise or dolphin. The attitude was thus comparable with that of a human swimmer making use of breaking waves for surf-riding.

A number of individual observers (e.g. McDonald, 1960) have described porpoises playing around the bows of small power boats in the English Channel. Here the bow wave appears to be too small to give an easily sustained free ride, and these porpoises tended to fall out of the wave and be left behind. The animals were, however, also observed to be rolled tail over head in the wave if the head sank too deeply ; i.e. they were somersaulted in exactly the same way as a surf-rider who does not maintain an adequate lift forward.

The character of the bow-wave varies with such factors as the hull form of the ship and its speed. The wave is created by water displaced by the advancing bow being thrown forward over the water immediately ahead. The height of the wave will be related basically to the displacement of the ship, its speed and bow form. Scholander's measurements of a wave are satisfactory so far as they go, but they represent only the picture of a slow moving ship. With faster speeds the front slope becomes steeper, whilst the water at the crest moves so rapidly that it is thrown forward over the front slope. Thus the important features are lift in the leading part of the wave, as Scholander shows, and a considerable forward velocity at its crest. In a fast moving ship, such as a destroyer, the volume of water thrown forward is considerable, so that the fast moving part of the wave is not limited to a thin layer at the crest ; it extends much deeper into the wave, the velocity decreasing with the

distance from the crest. Ahead of the wave, as Scholander has shown, the thrust of the water would be against the porpoise.

As our observations show, the porpoise presents the under surface of its tail to the rapidly moving water at the crest of the wave whilst lying at the surface ahead. Its problem therefore is to prevent its head from being forced down into the water ahead of the wave, as is found by human surf-riders. Human surf-riders keep themselves at the surface either by getting lift ahead from a surf-board or from the palms of the extended hands. Porpoises, like humans, must keep at the surface ahead of the wave, and, as has been observed, can be somersaulted if forward lift is not maintained. Although from our observations we are unable to prove the point, we believe that the flippers are carried in such a way that they could act sufficiently effectively as hydroplanes to maintain the required forward lift. Certainly observations on the swimming mechanism of the dolphins at Marineland, Florida, have convinced one of us (K.M.B.) of the remarkable efficiency of the foreflippers as hydroplanes ; very small changes in pitch produce surprisingly large changes in direction of the animal, even at relatively slow speeds. One may question the porpoise's ability to make use of the forward thrust at the wave crest on its tail flukes, but to do so would be a denial of the animal's ability to use these same flukes for swimming. Man's own ability to move forward in this way in a breaking wave without even tail-flukes or such an efficient hydrodynamic form as the porpoise is proof of what is possible. So far as the human surf-rider is concerned, the essential physical factors are that the legs and feet should remain in the rapidly moving part of the wave (or else he is left behind) and secondly that he should maintain himself at the surface of the water with sufficient lift anteriorly (or else he will be bowled over, the head being thrust under the water whilst the feet go on). For wave riding positive buoyancy thus appears advantageous, and a porpoise is well able to maintain this in life.

It can of course be argued that the breaking wave used by human surf-riders differs materially from the bow wave used by the porpoise, but in fact there is a striking similarity. Free swimmers (Byrne & Shenton, 1960) about to be picked up by boats going at speed testify to the forward propulsive effect of the bow wave which they have to pass through before being picked up.

These observations on the phenomen of wave riding porpoises thus go to confirm Scholander's suggestion that the animal may be making use of the characteristics of the bow wave, a contention for which he attempted to find experimental support. Scholander's explanation does not, however, make sufficient point of the essential breaking character of the bow wave, for, as has been described, wave riding has only been observed close to the bow in breaking water.

ACKNOWLEDGMENTS

We would like to thank a considerable number of people including Royal Naval and Royal Marine personnel, in addition to those named, for information and help on matters involved in this paper. One of us (K.M.B.) would like to thank the Florida State Museum (University of Florida), Dr J. C. Dickinson

Jr., Marineland Research Laboratories and Mr F. G. Wood Jr. for the opportunity to study dolphins in Florida, and also the University of London Research Fund for photographic and travel facilities. Certain observations were made during Naval Service, and are published with Admiralty permission.

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EXPLANATION OF PLATE

This photograph of a bow-riding dolphin provided by Dr H. J. Taylor of the Royal Naval Physiological Laboratory, was taken from a whaler of the Hector Whaling Company. It gives visual confirmation of the ideas expressed in this paper. The tail is in the breaking part of the bow-wave of the ship and the fore part of the animal is at the surface ahead of the crest. The direction of the waves arising from the dolphin itself is significant and indicates that the water even ahead of the wave crest is moving quite rapidly forwards past the animal.

Dolphin riding a bow wave.

SOME OBSERVATIONS ON THE BREEDING SEASON OF THE HEDGEHOG AND THE REARING AND HANDLING OF THE YOUNG

BY

B. MORRIS

Zoology Department, Nottingham University

[Accepted 14th June, 1960]

The breeding season of the hedgehog extends into late August and early September and lactation may continue very late into the year. The incidence of loss of embryos after implantation is low and is estimated at 3·3 per cent in the small sample recorded. The minimal duration of pregnancy in this species is thirty-one to thirty-two days, with a probable maximum duration of thirty-nine days. Observations on the rearing of the young and on the handling of the young for experimental purposes are reported.

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INTRODUCTION

Previous records of hedgehogs having been bred in captivity are few. Herter (1938) obtained four litters from captive animals but gives no details of the methods employed in breeding them. Ranson (1941) provides detailed information concerning the methods used by him in obtaining seven litters in 1939–1940. Animals caught in 1938 were kept in laboratory cages and during the autumn and winter of 1938–1939 were maintained at summer temperatures in a constant temperature room. Variations in lighting intensity were introduced, and two of the females were given subcutaneous injections of human pregnancy urine. Under these conditions no breeding occurred, and early in 1939 some of these animals were removed to outside breeding pens. From them he obtained seven litters, but pairs which were kept in laboratory cages did not reproduce. At the commencement of the breeding season several oestrous cycles, often accompanied by copulation, occur before pregnancy is achieved (Deanesly, 1934).

The information contained herein has been obtained during studies on the structure and development of the yolk-sac in this species (Morris, 1953, 1957). In an investigation of the transmission of passive immunity in the hedgehog, animals have been kept in captivity for long periods, and some success has been achieved in breeding them in captivity (Morris, 1959, 1960). Much valuable information has been obtained from Ranson's paper and from that of Edwards (1957). Animals kept in captivity have been fed on the diet recommended by the latter author.

BREEDING SEASON

The distribution of pregnancies in animals collected in the wild together with the observation that females in early stages of pregnancy may have well developed and recently functional mammary glands (Deanesly, 1934), indicate that hedgehogs may breed twice in one season. She records the following distribution of pregnancies in animals examined by her : May (7), June (6), July (3) and August (2). A lactating female filled on 12th October, with young weighing 110 gms., indicated the possibility that pregnancies also occur during September. The maximum number of foetuses observed was seven, with an average litter size of five, and she records as many as ten ruptured follicles in the two ovaries. Herter gives records of nine young in a litter. During May, June and July of 1949 and 1950 material was collected in Caernarvonshire and during May–September, 1954, in Nottinghamshire. A total of forty-two pregnant females were collected, distributed as follows : May (11), 21, June (6) 15, July (11) 27, August (1) 4, September (13) 25. The number in brackets indicates the number of pregnant females, followed by the total number of females caught during the month. In two females only, with four and two conceptuses respectively, all the foetuses were dead and were being reabsorbed. In two pregnant animals single embryos had died and were being reabsorbed, the remaining conceptuses appearing normal and healthy. These forty-two pregnancies contained a total of 191 post-implantation stages of which only eight were being reabsorbed. Deanesly records eleven pregnancies with fifty-one post-implantation stages, all apparently healthy, and assumes that since the average number of foetuses corresponds to the average number of ova ovulated there is little loss through ova failing to implant. These figures, taken together, are shown in Table 1 and indicate a post-implantation mortality of 3·3 per cent. The approximate and probably minimal nature of such an estimate has been demonstrated by Brambell (1948). This condition contrasts markedly with that in another insectivore, *Talpa europaea*, collected in Caernarvonshire in 1949 and 1950, and in Nottinghamshire in 1954, 1955 and 1956. In this species loss of entire litters occurs far more frequently (Table 1), and loss after implantation is as high as 25 per cent in this sample.

In 1958 females caught during the breeding season were kept in captivity until their litters were born. The fifteen litters obtained in this way yielded fifty-three young. Ten females mated in captivity in 1959 yielded thirty-two young. In these two groups the litter size at birth was not definitely ascertained. Although the females were examined each morning and evening the object of the examination was to determine whether a litter had been born. The females were disturbed as little as possible during this examination, and during the subsequent removal of young shortly after birth (Morris, 1960). Over 50 per cent of all the mature females caught in September, mainly in Nottinghamshire, were pregnant. Three females gave birth to young in mid-September and the latest date on which parturition occurred was 13th October, a female caught on 10th September which must have mated late in the first week of September. In the male spermatogenesis occurs between early April and late August and is at its height only between mid-April and mid-

Table 1—Litter size and loss after implantation in two species of insectivores.

Species	No. of pregnant females	No. of uteri containing :			No. of implanted embyros	No. of healthy embryos	Percentage mortality	Average litter size
		Post-implantation stages	Entire litters reabsorbing	Reabsorbing and healthy embryos				
Erinaceus europaea	53	53	2	2	242	234	3·3	4·6
Talpa europaea	70	66	14	2	268	201	25	3·9

June. Rapid testicular degeneration occurs during September (Skowron & Zajaczek, 1947). However, it is evident that mating occurs in late August and early September and that lactation may continue very late into the year.

THE DURATION OF PREGNANCY

Estimates of the period of gestation in this species have varied from four to seven weeks. Herter (1938) calculated the gestation period of three litters to be 34–49, 34–46 and 35–42 days. Ranson (1941) describes one female which was mated on 7th July littering on 16th August, a gestation period not exceeding forty days.

Thirty-two females were caught between early May and late September of 1958, and were kept in captivity. These females received immunizing injections during their period of captivity, and fifteen litters were obtained. Parturition invariably occurred during the night and eight of the pregnant females were captive for 30, 31, 31, 32, 33, 33, 34 and 37 days before their litters were born.

Many of the females which had been caught in 1958 were kept in hibernation throughout the winter and were placed in breeding pens in late April of 1959—three females and one male per pen. The pens were larger than those used by Ranson and measured $18 \times 12 \times 5$ ft. high. The wire netting was buried at least 1 ft. in the ground to guard against burrowing, and the walls of each pen were topped by baffle boards which projected inwards 7 in. to prevent the hedgehogs from climbing over. Ransom records that the greatest density at which breeding occurred was one animal to 24 sq. ft. whereas in the pens used here the density was one animal to 54 sq. ft. The females were weighed at intervals and were removed to separate outdoor cages when a marked increase in weight occurred. The ten litters which were obtained from these females were born 36, 37, 38, 39, 39, 44, 44, 44, 53 and 57 days after the females had been placed in the breeding pens. All the females had hibernated during the winter, but Ranson records four litters born to females which had not hibernated, and one litter from a female which had only hibernated for a short time. It apparently matters little whether the females hibernate or remain active in a warm animal house during the winter. The foregoing results indicate that Herter's original estimate of the duration of pregnancy, based on information obtained from three litters, is fairly accurate. The minimum duration is probably 34–35 days and the maximum duration 39 days.

The first litter that was obtained in 1959, born 36 days after the female had been placed in a breeding pen, was removed at birth and the serum of the young was sampled. The mother was brought into the laboratory, anaesthetized, and samples of the maternal serum and milk were obtained. Following this treatment this female was returned to the same breeding pen within a few hours, and a second litter was born to this female 38 days later. This was the only female from which two litters were obtained during 1959. Deanesly records six animals which had mated after lactation without becoming pregnant ; the condition of the vagina in females after parturition does not suggest a regular post-partum oestrus in this species and there is no oestrous cycle

during the first part of normal lactation. It is, however, clear that on the removal of a litter soon after birth a rapid return to breeding condition can occur with fertile mating at the first oestrus. From mid-August onwards nineteen females and seven males were kept in seven breeding pens but no litters were obtained.

REARING AND HANDLING OF THE YOUNG

Ranson reports that if the female is removed from the nest she will subsequently kill or desert the young. This was found to be so, and the necessity of removing one or more young from the litter shortly after birth has resulted in the loss of the remaining young. It is also reported that after five days the danger of subsequent loss after handling is considerably reduced.

There is evidently considerable variation in the subsequent behaviour of females which are disturbed with newly born young. The young of two litters were removed from the nest, one at a time, at different ages. The young were kept for a 2-hour period, at the end of which they were fed by stomach tube with homologous immune serum in a manner similar to that described for the rat (Halliday, 1955). They were then returned to the nest, and recovered 24 hours later and sacrificed. This procedure was successfully followed in one litter, the ages of the young animals on their initial removal from the nest being one, two, three, four and seven days, and was partially successful on a second litter at ages $1\frac{1}{2}$, $2\frac{1}{2}$ and $4\frac{1}{2}$ days. In this second litter the third young returned to the nest at $4\frac{1}{2}$ days old was dead on recovery 24 hours later and had been deserted by the mother. Entire litters, aged seven and eight days, have been removed, injected and returned to the nests without loss. At later stages, between 12–40 days, entire litters have been removed from their mothers, weighed, injected, and the serum of the young sampled by cardiac puncture under anaesthesia, and returned to the nests without loss. The serum of one lactating female was sampled seven days after parturition, after its removal from the single surviving member of its litter of three, two of which had previously been sacrificed. On being returned to the nest this mother suckled its remaining young which was eventually weaned. In one instance the serum of the mother and her three 22-days-old young were sampled by cardiac puncture and returned to the nest without loss. Experimental interference with litters between one and five days old is possible, but even when extreme care is exercised losses frequently occur. At seven days of age and older litters can be separated from their mothers, and vice versa, with excellent possibilities that normal suckling will ensue even after the mother and the young have been anaesthetized. No attempt has yet been made to foster suckling hedgehogs on to mothers other than their own.

The young of two litters have been observed eating solid food at 25 and 26 days of age, and at 22 days after parturition the mammary glands are full of milk. Herter records that a female suckled young which were 42 days old and he observed one young eating solid food at 21 days of age. Ransom recommends weaning at 38–40 days of age and those litters, and part litters, which have been bred here were successfully weaned at this age.

ADDENDUM

Thirteen litters were bred in captivity here during 1960, two of which were born 31 and 32 days after the females were run with males, so that the minimum duration of pregnancy in this species is shorter than that indicated by previous results.

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AN ANALYSIS OF THE FACTORS INFLUENCING THE CLUTCH SIZE OF THE KITTIWAKE

BY

J. C. COULSON AND E. WHITE*

Zoology Department, Durham Colleges in the University of Durham

[Accepted 14th June, 1960]

(With 4 figures in the text)

Clutch size of the kittiwake is influenced by the previous breeding experience of the female and also by the time of laying. Both of these factors play a part in determining the clutch size and the correlation between breeding experience and clutch size is not solely the result of older birds breeding earlier. The clutches laid by females breeding for the first time are, on average, smaller than those laid at the same time by more experienced breeders and are less influenced by the time of breeding. No female breeding for the first time has been found to lay three eggs. There is a correlation between the time of the onset of breeding in kittiwake colonies and the average clutch size. It is suggested that a progressive decrease in the clutch size as the breeding season progresses may be widespread in both passerines and non-passerines and probably occurs only in species which do not normally have two broods in a single breeding season.

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INTRODUCTION

It has been known for many years that the clutch size of a number of birds varies with the environmental conditions and also with the age of the female birds, and Lack (1954) has discussed these factors at some length. It has also been demonstrated that individual female birds tend to lay clutches in consecutive years which vary less in size than that of the population under investigation. This relative constancy of clutch size produced by individual birds has been shown to occur in the common swift *Apus apus* (Lack & Lack 1951), alpine swift *Apus melba* (Lack & Arn 1947), starling *Sturnus vulgaris* (Lack 1948), great tit *Parus major* (Kluijver 1951) and the velvet scoter *Melanitta fusca* (Koskimies 1957). Lack (1948, 1954) has cautiously suggested that this relative lack of variation in the clutch size of individual female birds may indicate a genetical difference which affects the clutch size of the individual. Kluijver (1951) does not hold this view for the great tit, and suggests that the consistency in clutch size of this species results from a

* Present address: Zoology Department, University of Liverpool.

tendency of each female to live in the same area in successive years, thus encountering consistent local differences in the environment, which, in turn, influence the clutch size every year.

Recently Koskimies (1957) has shown a close relationship between clutch size and the time of breeding of individual female velvet scoters, where birds breeding early lay more eggs than late breeding ones. He suggests that the difference was caused by a pair of linked genes, but he did not examine the possibility that there may be a direct relationship between the time of laying and clutch size, which could be independent of direct genetical control.

In this paper, data are presented which indicate that, although previous breeding experience (or age) affects clutch size, the time of breeding is the most important factor influencing the clutch size of the kittiwake *Rissa tridactyla*.

METHODS

The size of all clutches laid by kittiwakes in the North Shields, Northumberland colony (see Coulson & White 1958 a, b for details) have been recorded for eight years, together with the laying date of the first egg of each clutch. In addition, information on the clutch size and the time of laying of colour-ringed birds have been collected for six years.

Additional information concerning the clutch size of the kittiwake has been collected from the colonies at Dunbar, East Lothian and on Brownsman of the Farne Island group, Northumberland. Clutch size data from kittiwake colonies at St. Abbs, Berwickshire and from Inner Farne (Farne Islands) were provided by Mr I. J. Patterson and Dr E. Cullen respectively.

CLUTCH SIZE AND BREEDING EXPERIENCE

Coulson & White (1958 a) have shown that kittiwakes breeding for the first time lay a smaller clutch than those birds breeding for at least the third time. Data have been obtained for three more breeding seasons and all the relevant information is presented in Table 1. Birds breeding for the first

Table 1.—Relationship of clutch size to breeding experience of female kittiwakes. North Shields colony 1952–59 incl.

Clutch size	Breeding experience		
	First clutch	Second or third clutch	Fourth or more clutch
1	13	7	1
2	46	43	20
3	0	4	15
Mean	1·78	1·94	2·39

Note : The clutch size of certain female kittiwakes have been omitted from the above Table because they could not be put with certainty, into one of the four groups of breeding experience.

time lay 0·6 eggs less than birds breeding for at least the fourth time. No kittiwake breeding for the first time laid a clutch of three eggs, but there are now records of females breeding for the third and fifth time laying a clutch of only one egg (*c.f.* Coulson & White 1958 a).

During the six years in which the colour-ringed kittiwakes have been under observation, there has not been one instance of an individual female laying a second clutch in the same year. In only four instances did the entire clutch disappear, but these females did not re-lay. Many gulls will re-lay if their first clutch disappears, but this has not been observed in British colonies of kittiwakes, although Belopolski (1957) implies that it occurred in certain Murmansk colonies.

CLUTCH SIZE AND THE TIME OF LAYING

Table 2 shows the relationship between the date of laying the first egg of a clutch and the size of the clutch. The average clutch size decreased in a linear manner as the breeding season progressed. It is possible that one of the correlations relating clutch size to breeding experience (age) or clutch size to time of breeding may be fallacious, since it has already been shown that old kittiwakes also to tend to breed early (Coulson & White 1958 a). This possi-

Table 2—Clutch size of the kittiwake in relation to date of laying of the first egg. North Shields 1952–59 incl.

Clutch size	May			June		
	1–7	8–14	15–21	22–28	29–4	5–11
1	0	1	4	8	4	3
2	8	34	57	49	13	3
3	6	18	14	3	0	0
Total	14	53	75	60	17	6
Mean	2·43	2·32	2·13	1·92	1·77	1·50

Note : Clutches are only included in the above Table if the date of laying of the first egg had been determined within the error of ± two days.

bility was tested by determining the effect of the time of laying on three groups of female kittiwakes with different breeding experience. The results for females breeding for the first, second or third time and fourth or more occasion are shown in Fig. 1 and Table 3. There is a less pronounced relationship between the clutch size and the time of breeding in female kittiwakes breeding for the first time, than amongst those with greater breeding experience. It is also clear that female kittiwakes breeding for the first time lay, on average, fewer eggs (0·2 to 0·3 of an egg per female) than more experienced birds which lay during the same weekly period ($P<0{\cdot}01$). The difference between birds which were breeding for the second or third time and those which were breeding for at least the fourth time is not significant. These results show clearly that both previous breeding experience and the time of laying influence the clutch size of the kittiwake.

Further evidence of the influence of time of breeding on clutch size was obtained by comparing the clutch size laid during the same weekly periods in a number of colonies where breeding started later than at North Shields. It will be noticed in Fig. 2 that the lines for the Dunbar, St. Abbs, Brownsman and Inner Farne colonies all run parallel to that derived from the North Shields data. This supports the suggestion that the clutch size is influenced by the time of breeding.

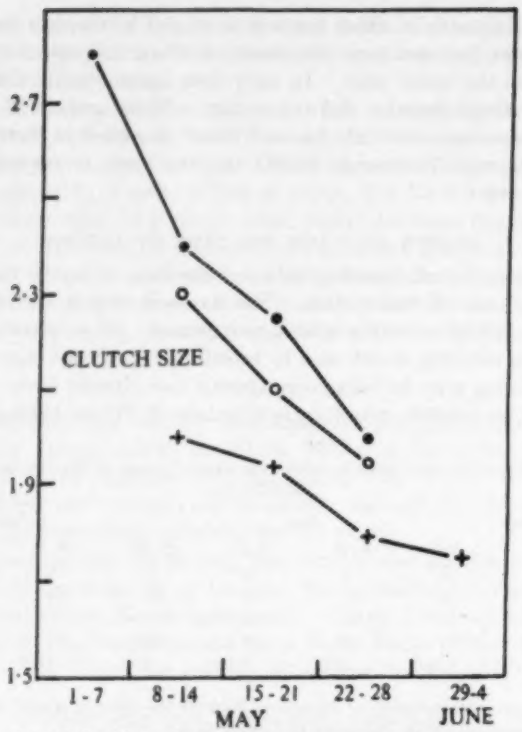

Fig. 1—The clutch size of the kittiwake in relation to previous breeding experience and the time of laying, based upon data in Table 3. Black dots: female kittiwakes breeding for at least the fourth time (42 clutches). Open circles: breeding for the second or third time (52 clutches). Crosses: breeding for the first time (48 clutches).

Table 3—Clutch size of the kittiwake in relation to previous breeding experience and the time of laying. In each column the number of clutches of one, two and three eggs are given from left to right, separated by commas. Dates on which there are less than five clutches recorded are put into brackets and these are not shown in Fig. 1.

Date of laying the first egg

	May				June	
	1–7	8–14	15–21	22–28	29–4	5–11
Females breeding for the first time	(0, 0, 0)	0, 5, 0	1, 15, 0	4, 15, 0	2, 6, 0	(1, 1, 0)
Females breeding for the second or third time	(0, 1, 1)	0, 17, 7	1, 16, 3	3, 14, 2	(1, 3, 0)	(0, 0, 0)
Females breeding for at least the fourth time	0, 1, 4	0, 11, 7	1, 14, 7	0, 7, 0	(0, 1, 0)	(0, 0, 0)

Note: Most of the above clutches are from kittiwakes breeding at North Shields but data on thirty clutches laid at Dunbar are included.

Another point of interest is that the later breeding colonies have, for each weekly period, an average clutch size approximately 0·1 greater than that recorded at North Shields (the difference between North Shields and the other colonies combined just reaches the 0·05 probability level).

Coulson & White (1960) have shown that the last eggs to be laid in these colonies appear at about the same time. Considering this and the relationship shown in Fig. 2, it can be implied that there may be a relationship between the time that laying starts in a colony and the average clutch size in that colony. As Table 4 shows, there is a close relationship between the average clutch size and the date on which 10 per cent of the breeding pairs have laid their first egg. Data collected in Arctic Russia and published by Belopolski (1957) also appear to fit this relationship.

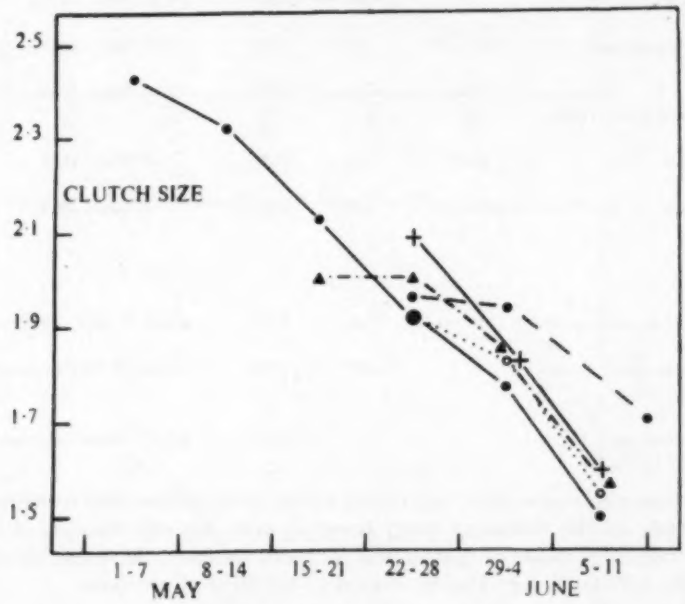

Fig. 2—The clutch size of the kittiwake in relation to the time of laying in five colonies. Black dot and continuous line—North Shields colony : Black dot and dashes—St. Abbs colony (130 nests) : Crosses—Dunbar warehouse (47 nests) : Open circles—Brownsman colony (110 nests) : Triangles—Inner Farne (55 nests). Data from Inner Farne from Cullen (pers. comm.) and majority of data from St. Abbs from Patterson (pers. comm.).

At North Shields the average annual clutch size of the kittiwake has remained remarkably constant, varying between 2·00 and 2·27 eggs over eight breeding seasons (Coulson & White 1958 b). Likewise the onset of breeding has been similarly consistent and the first egg to be laid in this colony appeared between 3rd and 9th May inclusive in each of the eight breeding seasons. The onset of breeding and the annual clutch size within a single

kittiwake colony is apparently much more variable within the Arctic Circle and Belopolski (1957) has reviewed much of the information on the breeding season. He also quotes an instance where the average clutch size of the kittiwake in a Murmansk colony changed from 2·33 to 1·53 eggs in consecutive years. From his discussion of other sea-birds in the area, it is clear that the

Table 4—Mean clutch size and start of breeding in certain kittiwake colonies.

Colony	Year	No. of nests examined	Mean clutch size	10 per cent of nests in colony with eggs
Great Britain				
North Shields	1952–59	230	2·07	13 May, 1958
Inner Farne (Cullen 1957)	1953–55	138	1·94	20–25 May, 1958
Dunbar (warehouse)	1958–59	45	1·89	21–25 May, 1958
St. Abbs (I. Patterson pers. comm.)	1957	96	1·87	29 May, 1958
Brownsman, S. E.	1958	110	1·86	23 May, 1958
Brownsman, N. E.	1955, 58	47	1·61	1 June, 1958
Foreign				
Denmark (Løppenthin 1945)	1943–44	117	2·18	about 7 May, 1945
Russia (Murmansk Coast) (Belopolski 1957)		557	1·96	about 20 May (average year)
(Novaya Zemlya) (Belopolski 1957)		—	1·6–1·7	after 9 June (average year)

first of these two years, 1937, was one in which most species bred exceptionally early, while in the following year, breeding was delayed because of a late thaw. Thus it is possible that at the northern limits of its range, the clutch size of the kittiwake may also be related to the time of breeding.

CLUTCH SIZE OF INDIVIDUAL FEMALE KITTIWAKES

The clutch size of twenty-one female kittiwakes which have laid four or more clutches are shown in Table 5. An analysis of variance between the clutches laid by individual females and that between females, indicates that individual females show less variation in their clutch size than did all of the females examined ($P<0·01$).

There are thirty-five instances where the clutch size of individual female kittiwakes changed in successive years and thirty of these showed either earlier breeding and an increase in clutch size or later breeding and a corresponding decrease in clutch size. The remaining five instances did not fit this pattern. By chance, it would be expected that half of the thirty-five instances

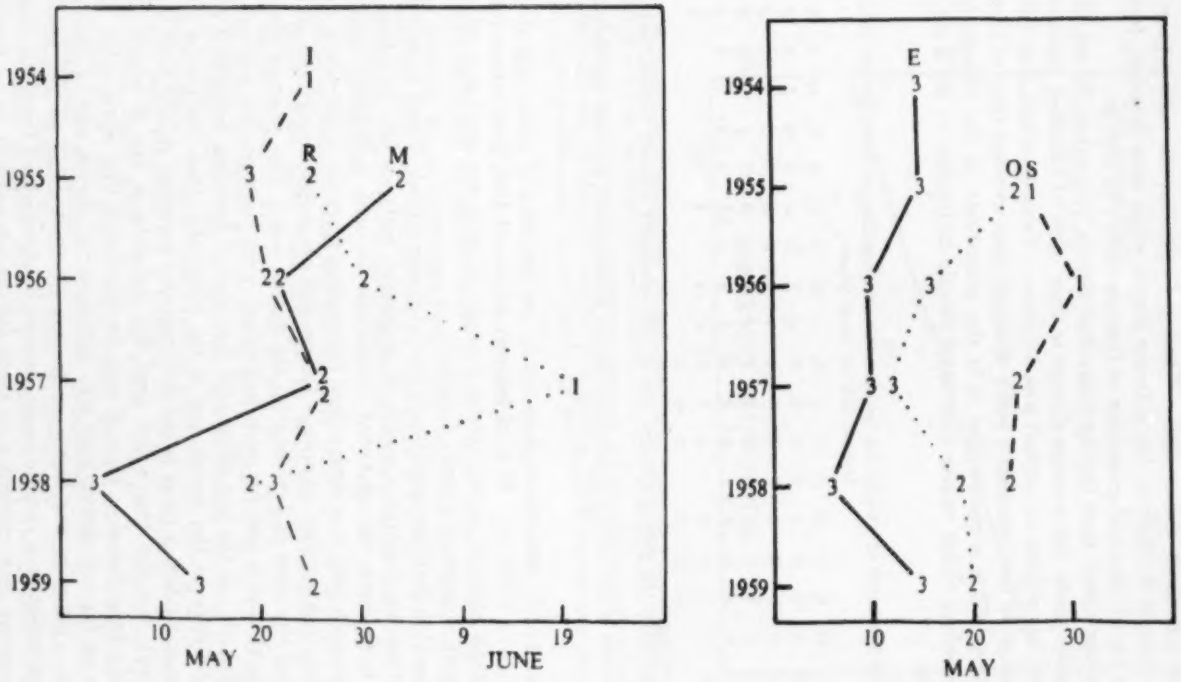

Fig. 3—The relationship between the time of laying and the clutch size of six female kittiwakes in successive years. The letters at the top of the figure correspond to those in Table 5.

would disagree with this pattern and the observed proportions are significantly different ($P<0.01$) suggesting that the time of breeding of individual female kittiwakes influences clutch size. When a female breeds earlier than in a previous year, it is likely to lay a larger clutch while later breeding tends to lower the clutch size and examples of this are shown in Fig. 3.

Where the clutch sizes laid by individual female kittiwakes did not change in successive years, the average change in their time of breeding (irrespective of whether it was later or earlier) was 6·5 days. Females which laid different sized clutches in two successive years changed their average time of breeding by 9·2 days. This suggests that it is the magnitude of the change in the time of breeding which causes individual female kittiwakes to lay a different clutch size.

Table 5—The clutch size of twenty-one female kittiwakes breeding at North Shields which have laid in four or more years.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
2	2	2	2	3	2	3	2	1	2	2	2	2	2	2	2	2	2	1	2	2
2	3	2	2	3	3	3	2	3	–	2	2	2	2	3	1	2	2	1	2	1
1	2	2	2	3	3	3	2	2	2	2	2	2	2	3	2	1	1	2	2	1
2	2	2	2	3	3	3	2	2	3	2	2	3	2	2	3	2	2	2	2	2
	2	1		3	3	3		3	2	2	2	3		2	3				3	
	3			3	3	3		2	2	2										

The clutches on the same horizontal line do not necessarily indicate clutches laid in the same year.

The variation in the clutches of individual females is significantly less than that between the females ($F=4·7$ with 20 and 94 d.f., $P<0·01$).

Certain female kittiwakes consistently lay clutches of three eggs (females E, F and G in Table 5). It is of interest to record that these three females changed their time of laying by an average of only 3·8 days and all three females were consistently early breeders.

It is possible that the consistency of clutch size already found in individual female kittiwakes may be a result of consistent early or late breeding. To test this hypothesis, the expected clutch size for each individual female (in Table 5) in each year was determined by reading from the appropriate line in Fig. 1, thus making due allowance for previous breeding experience and the influence of the time of breeding on the clutch size. The average observed and expected clutch size for each individual were then plotted against each other in Fig. 4. If the age effect and the time of breeding accounted for all of the variability in the clutch size of the kittiwake, then the points should have fallen along line A (that is the observed and expected should have tended to be equal), but the line which best fits the data is line B which differs significantly from line A. Thus it may be concluded that some other factor or factors so far not determined also influence the clutch size of individual kittiwakes. Whether the factor or factors involves some as yet unknown external stimulus or a genetic basis, cannot be determined from the existing data. However, it is evident that these factors are unlikely to be related to the breeding experience of the individual female kittiwakes or to the time of breeding.

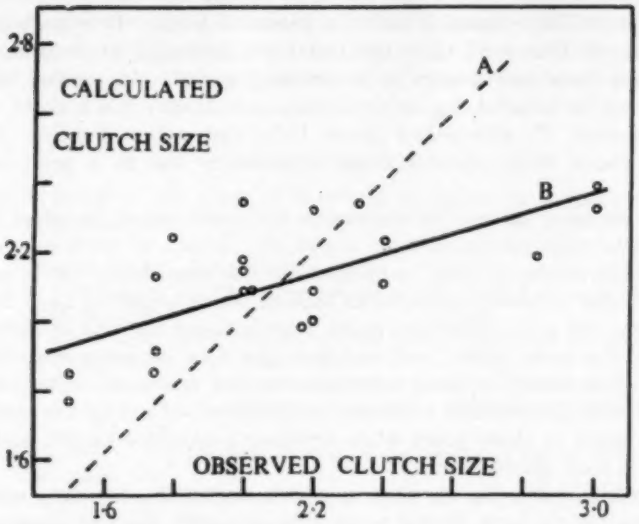

Fig. 4—The relationship between the average clutch size of individual female kittiwakes (shown in Table 5) and that calculated for each female. The calculated value was obtained by reading off Fig. 1 according to the previous breeding experience and the recorded time of laying for each clutch laid, and then obtaining an average value for each female.
Line A ; expected relationship, line B ; best fit to data.

DISCUSSION

The clutch size of the kittiwake is now known to be influenced by at least three factors, (i) previous breeding experience, (ii) the time of laying, and (iii) another factor or factors (which may have a genetical basis) which cause certain individuals to lay a consistently higher or smaller clutch than might be expected by chance.

Female kittiwakes breeding for the first time lay, on average, fewer eggs than birds which have bred before. In addition, older kittiwakes tend to breed earlier (Coulson & White 1958 a) and this, linked with the effect of the time of laying on clutch size, tends to cause older birds to lay larger clutches.

The average clutch size of the kittiwake decreases regularly throughout the breeding season. Similar relationships between the time of laying and clutch size have been reported for a number of birds including the great tit *Parus major* (Lack, 1950, 1956 ; Kluijver 1951), blue tit *P. coeruleus* (Lack, 1950, 1956), coal tit *P. ater* (Lack, 1950, 1956), crested tit *P. cristatus* (Lack 1950), pied flycatcher *Muscicapa hypoleuca* (Haartman 1951), collared flycatcher *M. albicollis* (Löhrl 1957), spotted flycatcher *M. striata* (Summers-Smith 1952), common redstart *Phoenicurus phoenicurus* (Lack 1949) and starling *Sturnus vulgaris* (Lack 1948). Among non-passerines, this phenomenon has been recorded for the black-headed gull *Larus ridibundus* (Svärdson 1958), velvet scoter *Melanitta fusca* (Koskimies 1957), and the redhead *Aythya*

americana (Low 1945). It would therefore appear that this relationship may be common in both passerine and non-passerine birds. It is perhaps worth commenting at this stage upon the fact that, normally, none of the species listed above have two broods in a breeding season. In species which are normally double brooded, e.g. robin (*Erithacus rubecula*) (Lack 1946), thrushes (*Turdus merula*, *T. philomelos*) (Snow 1955) and yellow bunting (*Emberiza citrinella*) (Lack 1954), the clutch size appears to rise to a peak and then decline.

While discussing the regular decrease in the clutch size of the great tit, Lack (1958) states :

> "This decline is fully confirmed by the new data, but it is, I now realise, due to three independent factors which ought to have been kept separate, (*a*) a big difference every year between the size of clutches laid during the main period and late layings, (*b*) a tendency for clutches to decrease in size to a small extent during the course of each main laying period and (*c*) a marked tendency for clutches laid during the main period to be larger in those years when breeding took place earlier, and smaller when it took place later."

In the kittiwake, the decrease in clutch size as the breeding season progresses has clearly been shown to be related to the time of breeding. Not only do kittiwakes lay a small average clutch in colonies where breeding is late, but individual female kittiwakes tend to lay a smaller clutch if they breed later, or a larger clutch if breeding is earlier than in the previous year. While the three stages mentioned by Lack could be recognized in the kittiwake, it is clear that only one factor, and not three, produces the relationship which exists between clutch size and the time of laying in the kittiwake.

It has not been possible to identify the cause of the relationship between time of breeding and clutch size, but it is obviously closely related to the actual date of laying. Since the onset of breeding in the North Shields colony was remarkably constant over eight breeding seasons, it is likely that increase in daylight may be the effective agent. Since the clutch size of the kittiwake does not appear to vary over the geographical range of this species, it should be possible to test this hypothesis by collecting data of the relationship between clutch size and the time of breeding from more northern regions where the increase in daylength is more rapid.

ACKNOWLEDGMENTS

Our thanks are due to Professor J. B. Cragg for help throughout the study and for criticising the manuscript.

The authors would also like to thank Dr E. Cullen and Mr. I. J. Patterson for unpublished data on the clutch size of the kittiwake recorded at Inner Farne and St. Abbs. We are also grateful to the management of Smiths Dock Co. Ltd., and Thomas Bernard Co. Ltd. for permission to study the kittiwakes which nest on their buildings at North Shields and Dunbar respectively, and also for the protection which they afford these colonies. The Farne Island Committee granted us permission to study the kittiwake colonies on the Brownsman ; a privilege which was greatly appreciated.

During part of the study, the authors held Nature Conservancy Studentships, while subsequently, J.C.C. held a Senior Research Studentship from the Royal Commission for the Exhibition of 1851. The Durham Colleges Research Fund also made a grant towards the travelling expenses incurred in the above study.

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ANNUAL VARIATIONS IN GROWTH AND DENSITY IN NATURAL POPULATIONS OF FRESHWATER SNAILS IN THE WEST OF SCOTLAND

BY

W. RUSSELL HUNTER

Department of Zoology, University of Glasgow

[Communicated by Dr J. D. Robertson—Accepted 11th October, 1960]

(With 4 figures in the text)

Surveyed over nine years, stable populations of *Ancylus fluviatilis*, *Physa fontinalis* and *Lymnaea peregra*, all with annual cycles, showed variation from year to year in mean size and in population density at the breeding season. This variation in adult mean size is about twice as great in *L. peregra* (i.e. approximately $\pm 17{\cdot}5$ per cent) as in the other two species. Fluctuations in population densities at breeding can be five-fold in *Ancylus* and *L. peregra* and three-fold in *Physa*. Annual variations in assessed productivity (as volumes of molluscan tissue per unit habitat) can be over seven-fold in *Ancylus*, more than three-fold in *Physa*, and over eight-fold in *Lymnaea peregra*.

With exceptions, there is general agreement between the annual figures for the different species, and they can be correlated with certain of the weather conditions prevailing during the preceding year. Severity of the winter appears the most important climatic cause of these molluscan fluctuations, particularly in *Physa* and *L. peregra*. Annual variations in *Ancylus* seem more closely related to spring sunshine, and a possible trophic basis is suggested for this difference between the species.

In relating this to other studies the interaction of external and endogenous factors in controlling life cycles is briefly considered. It is suggested that the plasticity in growth cycles and reproductive behaviour shown by freshwater snails is of fundamental selective value. Measurements of variations in growth and density in molluscan populations are proposed as a means of assessment of annual variations in total organic productivity of fresh waters.

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INTRODUCTION

Even within a relatively stable population of any freshwater snail, the average size attained by the adults when they begin to breed varies from year to year. This has been discussed using data for four years only for *Ancylus*

fluviatilis (Hunter, 1953 a). Other work has shown that the population density of such snails also varies from year to year. This present paper deals with data on growth and density for populations of *Ancylus fluviatilis* and *Lymnaea peregra* from 1949 to 1958 and of *Physa fontinalis* from 1953 to 1958. The records are nearly complete and continuous with a major exception in the 1954 season : no samples were collected for measurement, and no counts of density made in that year. It should be stated that the results and samples for the earlier years of this survey (those from 1949 to 1955) were not collected specifically for the present study of annual variation, but were part of the material accumulated during other work on the ecology and respiration of these snails (Hunter, 1953 a, b, c, 1957). The data presented and discussed covering the last three years were collected specifically for this survey. The three populations considered are particularly suitable for a study of annual variation in growth and density, since it is known that within them the annual cycle of life-history does *not* vary from year to year. In particular, the time of maximum reproductive activity does not vary by more than a few days from year to year, although it can vary considerably in other populations of these species, and in other species of freshwater gastropods (Hunter, 1961). Estimates are calculated of productivity in each year for the three species. The results are discussed in relation to known annual variations in weather conditions, and also more generally.

The work was carried out in the Department of Zoology, University of Glasgow, and at the Freshwater Laboratory, Glasgow University Field Station, Rossdhu, Loch Lomond ; and forms part of a series of investigations on the physiology and ecology of freshwater snails begun in 1948. Final calculations and preparation of this paper were done in 1958–59.

METHODS AND POPULATIONS STUDIED

The population of the freshwater limpet *Ancylus fluviatilis* considered here also provided the greater part of the results in an earlier paper on growth in this species (Hunter, 1953 a). This population lives in a relatively mesotrophic, " highland " stream, the Upper Craigton Burn, north of Glasgow. It is a stream which is typical of the many in which *Ancylus fluviatilis* is the dominant mollusc. Since earlier results from this population have been attributed erroneously to Loch Lomond, by other authors (Geldiay, 1956 ; Duncan, 1959) it is worth stating again that the Upper Craigton Burn is a tributary of the Allander Water, which is in turn a tributary of the River Kelvin, and does not form part of the Loch Lomond catchment area, although it lies less than two miles from the water-shed of that catchment area. Normally, each sampling has been confined to a stretch of stream less than four metres long. The samples of 1949 to 1952 were all taken from the same stretch but during 1953 sampling was moved some 60 metres upstream. Comparative samples taken at the same time in several months from both stations showed no significant differences, and all the later years' samples were taken at this second station. At the sampling station the stream has normally a width of 1·7 m. and an average depth of 15 cm., its rate of flow is normally

about 52 cm. per second (surface), and although its temperature falls to 0°C in winter, it has not been observed to rise above 16·2°C in summer.

The populations of *Lymnaea peregra* and *Physa fontinalis* considered here live in the " littoral " zone of Loch Lomond on the northern side of Auchentullich Bay near the Field Station. Most of the data for *Lymnaea* are drawn from that part of the shore where migrations were studied (Hunter, 1953 b) immediately south of the Field Station. All the data for *Physa* and some data for *Lymnaea* are drawn from a strip of shore which was marked out with iron pegs as a transect area for snails in 1952 and which lies about 350 yards (320 metres) north of the Field Station. The first locality is later referred to as the " Old " sampling station, the second as the " New " station. Both lie on erosion beaches of relatively large stones lying on firm-packed sand or clay. *Lymnaea peregra* is usually the most abundant snail at the " Old " station, *Physa fontinalis* at the " New ". A full description of the distribution of these and other species in the different littoral zones of Loch Lomond is given elsewhere (Hunter, 1957), but certain differences between the habitats must be noted. At the " Old " station, the shore is typical of the emergent zone in Loch Lomond with a " cobble-stone " substratum. At the " New " station, the substratum is intermediate between the typical cobble-stone beach and the sward of *Littorella uniflora* which is more characteristic of the zone immediately below the true emergent region. That is, unlike conditions at the " Old " station where there is little or no rooted vegetation, at the " New " station the stones are separated by patches and strips of *Littorella* turf (with occasional plants of *Isoetes lacustris* and *Lobelia dortmanna*). These types of substratum have been illustrated by underwater photographs (Hunter, 1953 b).

In almost all the records for all three species the population densities were assessed and the growth samples were collected for measurement within a few days of the end of May each year. The only irregular cases are two in 1955, where the samples were collected three weeks late. The actual data from these samples are first presented unaltered below, but in subsequent comparisons the values for these two late samples are adjusted to an " end-of-May " level. This is a particularly suitable time of the year at which to make these annual comparisons. As noted elsewhere, these freshwater pulmonate snails are essentially *annual* in life-cycle, the majority of adults dying very soon after spawning (see Hunter, 1953 a, 1957). The spawning time of the Craigton Burn population of *Ancylus* is from late April to mid-June. The inshore populations of *Physa* at Loch Lomond have their first peak of reproductive activity in May. Finally, although the spawning period of *Lymnaea peregra* in Loch Lomond is longer, a peak of activity is reached about the first week of June each year in such inshore populations. In the three species-populations studied, the dates of the begining of spawning, and of the peak in spawning activity, do not vary annually by more than a few days. Thus the growth samples taken at this time are certain to contain only over-wintered adults of near maximum growth for the population. Further, they are not likely to have been affected already by the size-selection which almost certainly operates during the rapid " dying-off " of the adults in the summer months. Sampling and assessment were usually carried out in one

day. The number of individual snails in each growth sample was never less than 30 and usually between 40 and 100. In those cases where more than 100 snails were collected in the sample, a random selection of 100 taken from it was measured. The samples of *Ancylus* were treated as in the previous growth survey, the periostraca being detached and stored in 70 per cent alcohol (see Hunter, 1953 a, for details). Measurement of the periostraca was carried out in fluid using a direct scale under a binocular microscope. A few measurements were checked by projection. The growth samples of *Lymnaea* and *Physa* were stored in 70 per cent alcohol, after fixation in either 10 per cent neutral formalin or 95 per cent alcohol, and were measured using a dial caliper. Again, a few smaller snails were also measured using a micro-projector. As the measurements were made, they were grouped in tenths of a millimetre (i.e. all shells between 8·25 mm. and 8·35 mm.) were recorded in the interval whose class mark was 8·3 mm.). All samples of all three species were thus measured to intervals of 0·1 mm. For *Ancylus* and *Physa*, the original class marks were used subsequently for the calculations of means and standard deviations, and for the histograms (Figs. 1 and 2). For *Lymnaea*, where the range of size is wider, even in such breeding samples, a modified grouping into class intervals of 0·2 mm. was adopted for calculations and for histograms (Fig. 3).

Population densities were assessed using the method described by Hunter (1953 a). It is difficult to make reliably quantitative estimations of the density of freshwater fauna on stony substrata, but, if comparative figures for only one or a few species are required, the problem is simplified. In using this method a sheet of paper with a marked area 50 cm. square was laid on the bank of the stream, or near the edge of the lake. Stones were taken singly from the habitat and the number of snails adhering to each counted. Each stone was laid on the paper and its greatest outline quickly sketched. Then the stone was returned to its place. The process was continued with other stones until the traced outlines, which had been fitted together like a jig-saw puzzle, filled the quarter square metre. No stones of less than one inch diameter were normally taken, but otherwise no special selection was made. In estimations of the density at each sampling, four or six such sheets were used. Density values for *Lymnaea peregra* only, for the years 1949–52 were obtained using a slight modification of this method (see Hunter, 1953 b) based on a larger number of smaller sub-samples. Although the figures given below are expressed as numbers of snails per square metre, these should not be regarded as absolute values of population density, but only as comparative figures. As a result of the method of estimating area of stones, each of the figures given of the number of snails or limpets per square metre is greater than the actual number of snails or limpets per square metre of exposed stone surface. For *Physa* and *Lymnaea peregra*, the figure given will also be greater than the number of snails per square metre of the lake bottom. On the other hand, for *Ancylus*, where only stones from the upper layer of the stream bottom were measured, the given figure is probably less than the actual number of limpets living on a square metre of the stream bottom. Nevertheless, this simple method yields reproduceable figures which can be

safely used in comparing population densities within one species at different times in the same habitat.

To allow comparisons of the annual productivity in these snails, an estimate of the " standing crop " at May/June each year has been calculated for each species. Although weights of snails are not available, the mean lengths of the samples have been converted to volumes for use, with the density figures, in preparing these estimates. For *Lymnaea peregra* and *Physa*, suitable conversion figures for adult snails are given in an earlier paper (Hunter, 1953 c). Estimation of the volume in *Ancylus* is dealt with below. It should be noted that each volume figure, used with the density to produce an estimate of productivity, is *not* in fact the mean figure for the volumes of the snails in each sample, but is the volume of a snail of mean length for that sample. Again, this means that the productivity figures, although they can be safely employed for *comparative* purposes, do not represent *actual* volumes of molluscan tissue per unit area (of stream or of lake bottom).

ANCYLUS FLUVIATILIS

One standard measurement was made on the detached periostraca of all samples of this species. This is the aperture length (AL), being the greatest dimension across the opening of the limpet-shell. For certain ratios mentioned later, other two measurements were made : first, the aperture breadth,

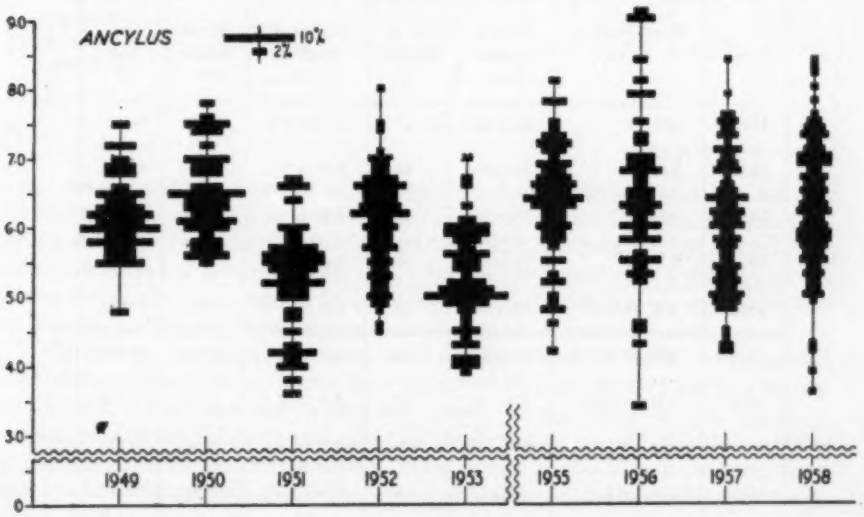

Fig. 1—Aperture-lengths (AL) in mm. of periostraca of annual samples of breeding *Ancylus fluviatilis* from the Upper Craigton Burn station ; for further explanation, see text.

measured at right angles to AL, and secondly, the shell height, being the maximum height of the shell measured from the plane of the opening. Both the aperture length and the aperture breadth can readily be measured, using

a binocular microscope or microprojector, when the limpet periostracum is lying in fluid with the aperture on a scaled surface. It should be noted here that in one earlier paper (Hunter, 1953 a) on the growth of *Ancylus*, this standard measurement (AL) was referred to as the "shell-length". In the present study and in other recent work (Hunter, 1961), it has been thought better to restrict the term shell-length to its application in turbinate-shelled snails like *Lymnaea* spp. wherein a very different dimension is implied. The histograms of Fig. 1 show the sizes in mm. of periostraca from samples of limpets taken near the end of May over nine years (1949 to 1958, less 1954), from the Upper Craigton Burn station. For comparative purposes the frequency in each class is shown as a percentage of the total number in the annual sample. A summary of the size data, including means and deviations, from these samples is given in Table 1. Data for the first four years (1949 to 1952) are already published (Hunter, 1953 a). It is obvious that the size of breeding *Ancylus fluviatilis* from this one locality varies considerably from year to year. It is also apparent from the histograms and from the column of standard deviations in Table 1 that the relative variability (the extent of variability of aperture length within each annual sample) also fluctuates.

Table 1—Summary of size data from nine annual samples of breeding *Ancylus fluviatilis*, Upper Craigton Burn station.

Year	Identification letter	Actual sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
1949*	AM/49	31/v/49	43	4·8 to 7·5	6·19	0·54
1950*	AM/50	1/vi/50	46	5·5 to 7·8	6·48	0·615
1951*	AM/51	26/v/51	44	3·6 to 6·7	5·22	0·763
1952*	AM/52	30/v/52	80	4·5 to 8·0	6·07	0·705
1953	AM/53/A9	29/v/53	75	3·9 to 7·0	5·23	0·684
1955	AM/55/R20A	1/vi/55	60	4·2 to 8·1	6·34	0·832
1956	AM/56/12P	2/vi/56	48	3·4 to 9·1	6·41	1·193
1957	AM/57/2P	30/v/57	100	4·2 to 8·4	6·03	0·939
1958	AM/58/14P	3/vi/58	100	3·6 to 8·4	6·27	0·927

*Data for these four years from Hunter (1953 a).

In Table 2 is given a summary of densities assessed by the method already outlined. With the exception of the year 1949, when no density determinations were made for *Ancylus*, these assessments were made each year at the time of collection of the growth samples (i.e. at the dates given in the third column of

Table 1), and at the same station on the Upper Craigton Burn. The total number of limpets removed in this survey, and even during more frequent sampling in the years 1949 to 1950 and in 1952 to 1953, is very small in relation to the total population in each year. In other words, it can be assumed that this sampling has not itself altered the population. In the year 1953, and in summer 1956, this point was further checked by comparing the population densities at the regular sampling station and at other parts of the Upper Craigton Burn. When, for each year the figures for density of adult limpets given in Table 2 are compared with the mean lengths of the adults from Table 1, there is no indication of an inverse relationship between size and density, i.e., breeding limpets are not necessarily bigger when there are fewer of them. Although an inverse density-dependent factor controlling size might reasonably

Table 2—Summary of density data for eight years for breeding *Ancylus fluviatilis*, Upper Craigton Burn station

Year	1950	1951	1952	1953	1954	1955	1956	1957	1958
No. of adults determined per sq. m.	518	132	324	168	n.r.	392	97	240	212
No. of egg-capsules determined per sq. m.	3,316	n.r.	n.r.	n.r.	n.r.	3,112	646	1,946	1,596

n.r. = no records available.

have been expected in such a strictly limited population as these limpets living in a highland stream, this is not so. In fact, in two of the years of relatively low density of breeding *Ancylus* (1951 and 1953), the mean lengths of samples of the limpets are also relatively low. In the third year of low density in the series (1959) the mean length is relatively high, but in this year the variability in size within the sample is higher than in any other year.

For five of the years, the numbers of egg-capsules of *Ancylus* were counted on the same stones at the same time as the adult limpets, and are also shown in Table 2. The relationship between density of egg-capsules and density of adults in samples taken at this point in the breeding season is fairly straightforward. Besides the counts shown in Table 2 from the Upper Craigton Burn station in different years, assessments of densities of adult snails and of egg-capsules have been made during the breeding season in populations of the same species in other localities. When numbers of egg-capsules are plotted against numbers of adults, egg-capsule density appears as directly proportional to adult density, over most of the range of densities encountered in the West of Scotland in different years. At adult limpet densities between 100 and 400 per square metre, the numbers of egg-capsules are at this stage usually about 7·5 times the number of adults. At very high densities (over 400 per square

metre) the number of egg-capsules per adult is lower. This is also true at low densities. The biological explanation must be complex, but it is likely that over-crowding is among the causes of lower egg production by adult limpets at high densities. Very low adult densities themselves suggest poor feeding conditions as a cause of lowered egg production. In the Upper Craigton Burn population, the first egg-capsules are usually laid about the third week of April and the main spawning is over by mid-June, although a few egg-capsules are laid until mid-July. The late-laid capsules contain less than one per cent of the eggs produced (Hunter, 1953 a). Repeated density assessments of adults and egg-capsules were carried out through the breeding season in 1950 and again in 1953 at the Upper Craigton Burn station and at the Green Burn, a tributary of the River Fruin, Dunbartonshire. Some data from 1950 are already quoted (Hunter, 1953 a). By the end of May in each year some five-eighths of the total egg production has already occurred. In *Ancylus* the average number of eggs per capsule is 3·93 (Hunter, 1953 a, and further unpublished results). Therefore, from the present data of annual samples, an individual limpet produces $7{\cdot}5 \times 1{\cdot}6 \times 3{\cdot}93$ eggs, i.e. 47·16 eggs per breeding season. This is closely comparable with the figure of 46 eggs contained in " about 12 capsules " which resulted from earlier work (Hunter, 1953 a). A field assessment made by Geldiay (1956) on populations in the Lake District resulted in a total number of about 50 eggs in " between 10 and 20 capsules, the number being more likely nearer the lower figure ". In his detailed laboratory study of basommatophoran egg-capsules, Bondesen (1950) gives figures for egg production in *Ancylus fluviatilis* which are even lower but of the same order as these. Thus the freshwater limpets lay markedly fewer eggs than most other freshwater pulmonate snails. The annual ratio of selection in stable populations of *Ancylus fluviatilis* is about 47 : 1, against about 1400 : 1 in *Lymnaea peregra* (Hunter, 1953 a, 1957). (In any such population, with a simple annual life-cycle and a limited breeding season, the " annual ratio of selection " is that which, for the known potential reproductive capacity, would allow the population to remain stable as regards population density from year to year.) It has been suggested (Hunter, 1956, 1957) that if *L. peregra* is compared with *Ancylus*, in the first, great phenotypic adaptability in behaviour is associated with a relatively high annual rate of selection, while in the other, inherited structural specialization is associated with a relatively low selection rate.

In Table 3 an attempt is made to assess the annual variation in productivity (in terms of *Ancylus*-tissue) of the Upper Craigton Burn. The only regular measurement of size in *Ancylus* was the aperture length (AL), measured on the periostracum. Before the comparative figures could be prepared, the linear measurements had to be converted to assessments of volume (as a closer approximation to mass). Now, in the Upper Craigton Burn and in similar highland streams in the West of Scotland, the proportions of an adult *Ancylus* are :— aperture length (AL) : aperture breadth : shell height =70 : 54 : 33. In this population the volume of an *Ancylus* therefore will closely approximate to the volume of a cone whose height (h) is 33/70 of the aperture length AL of the *Ancylus*, and whose mean radius (r) is 31/70 AL.

Table 3—Annual variation in mean lengths, calculated volumes, and assessed productivity for breeding *Ancylus fluviatilis*, Upper Craigton Burn.

Year	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
Mean length in sample mm.	6·19	6·48	5·22	6·07	5·23	n.r.	6·34	6·41	6·03	6·27
Calculated volume cu.mm.	23·01	26·39	13·8	21·69	13·88	—	24·72	25·55	21·27	23·91
Assessed productivity cu.mm./sq.m.	—	13,670	1,822	7,028	2,332	—	9,690	2,478	5,105	5,069

n.r. = no records available.

Thus the *Ancylus* volume $= \frac{1}{3}\pi r^2 h$

$$= \frac{\pi}{3} \times \left(\frac{31}{70}\,AL\right)^2 \times \frac{33}{70}\,AL$$

$$= \frac{\pi}{3} \times \left(\frac{31^2 \times 33}{70^3}\right) \times \left(AL^3\right)$$

$$= \frac{\pi}{3} \times 0{\cdot}09246 \times AL^3$$

$$= 0{\cdot}097 \times AL^3$$

Therefore in Table 3, each volume value shown is the product of this conversion factor 0·097 and the cube of each mean of aperture lengths. This conversion factor could not be used for populations from elsewhere in Britain, in which the shell proportions may differ, particularly in relation to shell height. A sample from the Borders, for example shows :— AL : aperture breadth : shell height =70 : 52 : 41 ; proportions met with in many more southern populations. On the bottom line of Table 3 are given values for the productivity of the *Ancylus* population in each year, being each the product of the

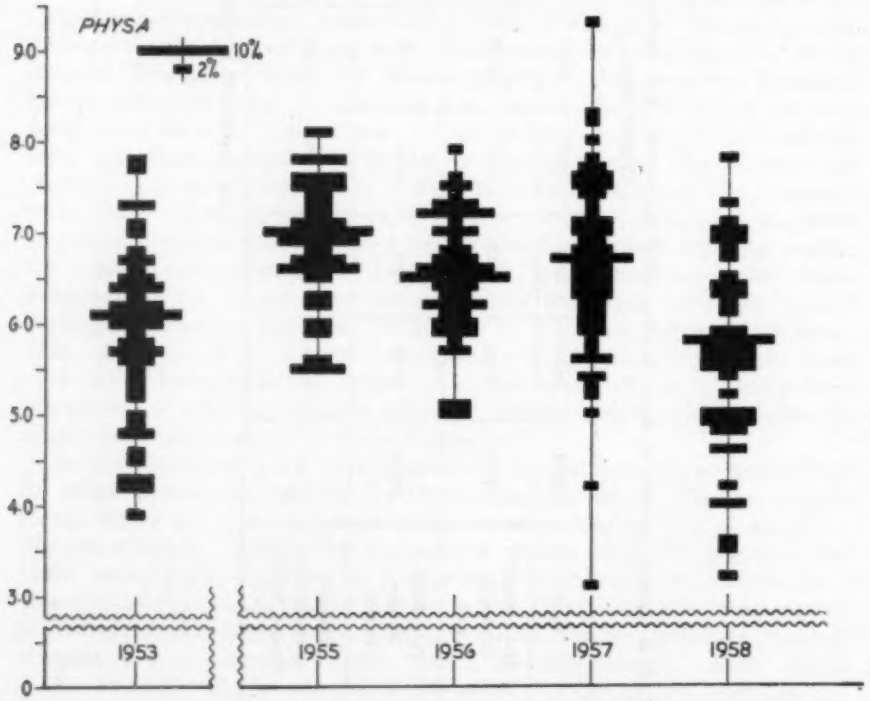

Fig. 2—Shell-lengths (SL) in mm. of annual samples of *Physa fontinalis* from the " New " littoral station, Rossdhu, Loch Lomond ; for further explanation, see text.

volume value calculated for the limpet of mean length and the value for limpet population density at the time. This productivity assessment can be regarded as expressing, for comparative purposes, volumes of *Ancylus*-tissue produced per square metre of the stream bottom, but for reasons stated above, they cannot be taken as *absolute* values for productivity.

PHYSA FONTINALIS

All growth samples were collected and all densities assessed for this species at the "New" littoral station at Rossdhu, Loch Lomond. The sampling area covered a strip extending along-shore for 20 metres, which is stable and of gentle slope (i.e. about 9 cm. per metre). Samples were taken from the water's edge to a depth of 0·5 metres, so that sampling could range over about 110 square metres of beach at any one level of the lake. The standard measurement made on the shells of *Physa* is termed the shell-length (SL). It is the maximum length of the shell from the apex of the spire to the peristome, or outer edge of the aperture. It is a measurement made conveniently with any type of external caliper, and particularly rapidly and accurately with an engineer's dial caliper. The histograms of Fig. 2 show the shell-lengths in mm. of samples of *Physa* taken near the end of May over five years (1953, and 1955 to 1958), from the "New" station. The frequency in each class is again shown as a percentage of the total number in each annual sample for comparative purposes. A summary of the size data from these samples, including means and deviations, is given in Table 4. It is obvious that, as in *Ancylus*, the size of breeding *Physa fontinalis* from this one locality varies much annually, and the extent in each year of variability of size also varies. The sample for 1955 was collected some three weeks later than usual. For further comparisons the value of the mean length for this sample can be adjusted to an "end-of-May" level. From other work (Hunter, 1961) the growth rate of adult *Physa* in inshore populations at Loch Lomond in the late spring and early summer is 0·82 mm. per four-week period. The mean

Table 4—Summary of size data from five annual samples of breeding *Physa fontinalis*, Rossdhu "New" littoral station, Loch Lomond.

Year	Identification letter	Actual sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
1953	AM/53/3	29/v/53	50	3·9 to 7·8	5·86	0·93
1955	AM/55/R21P	22/vi/55*	33	5·5 to 8·1	6·85	0·664
1956	AM/56/P3	31/v/56	59	5·0 to 7·9	6·52	0·653
1957	AM/57/12	5/vi/57	66	3·1 to 9·3	6·61	0·978
1958	AM/58/4	30/v/58	50	3·2 to 7·8	5·61	1·023

*Late sample, see text.

shell-length of this late sample is 6·85 mm., so that, with a deduction of 0·61 mm. for three weeks' growth, the value for mean length for breeding *Physa* in 1955 appears as 6·24 mm. in Table 6 and subsequent comparisons.

In Table 5 are summarized the density data for *Physa* for the same years at the same locality. The total number of snails removed in this survey, and during more frequent sampling in 1952 and 1953 is very small in relation to the total population of *Physa* in the whole "New" sampling area of approximately 330 square metres. It is about one-twentieth of the total area of similar beach in this one bay of Loch Lomond. Thus sampling has not itself altered the population. When the densities of adult snails are compared with the mean lengths given in Table 4, again in this species there is no sign of an inverse relationship. In fact, the year (1957) with maximum density of *Physa* is also the year of greatest mean size at the breeding season. Comparative densities of egg-masses for 1955 to 1958, counted with the adult *Physa*, are also shown in Table 5. The method of assessing egg-masses results in figures more approximate than those for egg-capsules of *Ancylus*. At this sampling station in these years *Lymnaea peregra* has been present (and counted) in each density assessment. Usually, both species are actively laying eggs at that time. In the field, it is difficult to segregate the egg-masses of the two species, and only a total number of egg-masses per quadrat of stones was recorded. A smaller number of typical stones (usually about eight) was retained, and the egg-masses from these were examined under a low power microscope, and allocated to the appropriate species. The figure for egg-masses in Table 5 is actually that part of the total counted per square

Table 5—Summary of density data for five years for breeding *Physa fontinalis*, Rossdhu "New" littoral station, Loch Lomond.

Year	1953	1954	1955	1956	1957	1958
No. of adults determined per sq. m.	76	n.r.	81	41	123	62
Approximate no. of egg-masses per sq. m.	n.r.	n.r.	469	324	1,173	460

n.r. = no records available.

metre allocated to *Physa*, on the basis of a *Physa* to *Lymnaea* egg-mass proportion, which had been determined from the smaller sub-sample of egg-masses examined in the laboratory. For example, in 1955 and 1957 the egg-mass ratios were *Physa* : *Lymnaea* = 5 : 2 and = 3 : 1 respectively. In 1957, the ratio was 6 : 3 : 1 for *Physa* and two distinct types of *Lymnaea* egg-masses. As a result of this approximation and the smaller number of years covered, it is difficult to comment on any relationship between adult density in *Physa* and number of egg-masses. However, it seems unlikely that there is any falling-off in egg-production at high adult densities, as in *Ancylus*. Over

all the samples counted, the numbers of egg-masses per adult vary considerably, but the average figure is 8·6 at this stage. The mean number of eggs per egg-capsule in *Physa* living inshore in Loch Lomond is 15·2, and the density figures at this time correspond to three-quarters of the total egg-production for the breeding season. Thus, individual snails produced an average of $8{\cdot}6 \times 1{\cdot}33 \times 15{\cdot}2$ eggs, i.e. 174 eggs through the breeding season. These figures for egg-production for *Physa* at Loch Lomond accord well with other

Table 6—Annual variation in mean lengths, calculated volumes, and assessed productivity for breeding *Physa fontinalis*, Rossdhu " New " littoral station, Loch Lomond.

Year	1953	1954	1955	1956	1957	1958
Mean length in sample mm.	5·86	n.r.	6·24*	6·52	6·61	5·61
Calculated volume cu.mm.	26·76	—	32·32	36·86	38·41	23·48
Assessed productivity cu.mm./sq.m.	2,034	—	2,618	1,511	4,724	1,456

n.r. = no records available.
*Adjusted to end-of-May value, see text.

published results. Bondesen (1950) reports up to 20 eggs per egg-mass in this species, but does not give a figure for total egg-production per snail under natural conditions. In the recent careful field study of *Physa fontinalis* by De Wit (1955) at Botshol near Utrecht, the over-wintering generation produced an average of 10 egg-masses per snail, with an average number of 16 to 18 per mass. This is particularly close to the rate of egg-production in the Loch Lomond inshore population.

As for *Ancylus*, annual variation in productivity in *Physa* has been assessed in Table 6. In *Physa*, relationship between volume and shell-length had already been calculated (and also determined empirically), in earlier work on respiration in this species (Hunter, 1953 c). The volume values of Table 6 are the cubes of the mean lengths, each multiplied by 0·133, which is a suitable conversion factor for adult *Physa*. Values for the productivity of this inshore population of *Physa* at Loch Lomond for each year are given in the bottom line of Table 6. Each of these productivity values is the product of the calculated volume of a snail of mean length and the population density of adult snails at the time. For comparative purposes, each productivity value expresses the volume of *Physa*-tissue produced per square metre of the lake shore for that year. For the reasons elaborated earlier, such values cannot be taken as *absolute* measures of productivity.

LYMNAEA PEREGRA

The results presented for this species are somewhat complicated in that two distinct stations in the littoral zone at Rossdhu, Loch Lomond, were used both for the collection of growth samples and for the assessment of snail densities. Results for *Lymnaea peregra* referred to the "New" littoral station derive from the same pegged-out area of shore which provided the results for *Physa fontinalis* already presented. At the "New" station, growth samples were collected from the same areas over which density assessments were made. At the "Old" littoral station, density assessments were made on a strip of shore from which no growth samples were ever taken (see Hunter, 1953 b). The "Old" station growth samples were taken from similar ground immediately to the south of the main density counting strip.

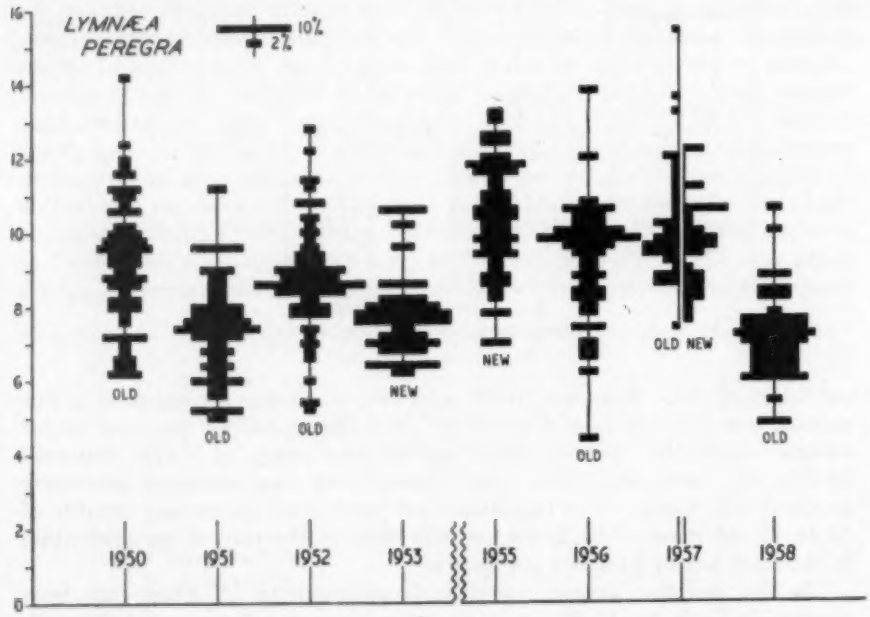

Fig. 3—Shell-lengths (SL) in mm. of annual samples of breeding *Lymnaea peregra* from the "Old" and "New" littoral stations, Rossdhu, Loch Lomond; for further explanation, see text.

Environmental differences between the "Old" and the "New" stations have been mentioned above, and detailed elsewhere (Hunter, 1953 b, 1957). It should be mentioned here that the slope of the beach at the "Old" station (4·3 cm. per metre) is less than at the "New" (9 cm. per metre). *Littorella* turf occurs at the "New" station, and *Physa fontinalis* is, of course, common there. *Lymnaea peregra* is both more abundant, and of larger mean size, in the breeding season at the "Old" station.

The standard measurement made on the shells of *Lymnaea peregra* was again shell-length (SL), or maximum length from the apex of the spire to the peristome. As in the other two species, measurements were made to intervals of 0·1 mm., but in *Lymnaea* a modified grouping into class intervals of 0·2 mm. was adopted, for calculations and Fig. 3. Shell-lengths in mm. of the nine samples of breeding *Lymnaea* are shown in the histograms of Fig. 3. For comparative purposes the frequency in each class is again shown as a percentage of the total number in each annual sample, except in the case of the 1957 samples from " Old " and " New " stations shown as two distinct halves of a normal histogram. A summary of the size data from these samples, including means and deviations, is given in Table 7. Before considering complications introduced by the two sampling stations, it is obvious that, as in the other two species, the size of breeding *Lymnaea peregra* at any one station varies considerable. Samples for 1950 to 1952 are unlike all the other collections dealt with here, as they result each from collecting on more than one day, during work on migrations and respiration (Hunter, 1953 b, 1953 c).

Table 7—Summary of size data from nine annual samples of breeding *Lymnaea peregra*, Rossdhu " Old " and " New " littoral stations, Loch Lomond.

Year	Station	Identification letter	Actual sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
1950	Old	PR53/50	22–29/v/50*	66	6·1 to 14·1	9·15	1·716
1951	Old	PR53/51	26 & 27/v/51	44	5·0 to 11·2	7·38	1·346
1952	Old	PR53/52	28 & 29/v/52	74	5·1 to 12·8	8·75	1·421
1953	New	AM/53/5	29/v/53	31	6·2 to 10·6	7·81	1·152
1955	New	AM/55/R21L	22/vi/55†	51	6·9 to 13·1	10·35	1·539
1956	Old	AM/56/L3	31/v/56	43	4·3 to 13·8	9·19	1·625
1957	Old	AM/57/19	5/vi/57	39	7·4 to 15·3	10·21	1·531
1957	New	AM/57/15	5/vi/57	32	7·5 to 12·2	9·6	1·197
1958	Old	AM/58/9	30/v/58	45	4·7 to 10·6	7·12	1·142

*Three separate collections from this week taken together.
†Late sample, see text.

As regards size, they were, however, random, and comparable with other growth samples. As for *Physa*, the 1955 annual sample, from the " New " station, was collected three weeks later than usual. Its mean length can be adjusted to an " end-of-May " level. From other work (Hunter, 1953 b, 1961) the growth rate in late spring and early summer of adult *Lymnaea peregra* in inshore populations at Loch Lomond averages 1·23 mm. per four-

week period. The mean length of this late sample of *Lymnaea* is 10·35 mm., so that, deducting 0·92 mm. for three weeks' growth, the value for mean length at the usual sampling time would have been 9·43 mm. at the " New " station. For calculation of volumes and assessment of productivity, records for 1953 and 1955 were converted to corresponding values for the " Old " sampling station. For all the other years considered, actual records from the " Old " station were available, and for 1957 only the " Old " station records are subsequently considered here. When all pairs of samples of *Lymnaea* taken at the same time from the two stations are considered, the size of breeding adults at the " Old " station is 7·4 per cent larger than the size at the " New " station. Accordingly the mean shell-lengths for breeding *Lymnaea peregra* in 1953 and 1955 appear as 8·39 mm. and 10·13 mm. respectively in Table 9 and subsequent comparisons.

The density data available from 1949 to 1958 omitting 1954 for breeding *Lymnaea peregra* at both littoral stations are presented in summary in Table 8. At the " New " station densities are largely comparable to those of *Physa* and the sampling areas are the same. At the " Old " station no samples were collected from the restricted area where densities were assessed. Thus, in both cases, it can be assumed that sampling has not itself altered the population. Densities given for 1949 to 1952 differ from all other density figures in this paper, being mean densities of all assessments made for the first two metres offshore (i.e. generally in depths of less than 30 cm.), from mid-May to July. The figures given for these years in Table 8 are converted from the mean densities " per square foot " given in the earlier migration study (Hunter, 1953 b). They are thought to be reasonably comparable with the density figures for 1953 onwards which were obtained in exactly the same way as all other density figures in this paper. Again data have to be reduced to values corresponding to a single locality, and again figures are available for the " Old " sampling station for seven out of the nine years. From many comparative density assessments carried out at both stations on the same day, the density of adult *Lymnaea peregra* at the " Old " sampling station averages 2·38 times its density at the " New " one. Density figures for 1953 and 1955 are increased by this factor before being used to calculate productivity figures for Table 9, and subsequent comparisons. When these density figures in Table 8 for each year and station are compared with the mean shell-lengths of Table 7, again there is no trace of an inverse relationship between density and size. In fact, the years with smaller breeding *Lymnaea* have relatively low adult densities. When for each year, the *Lymnaea* and *Physa* results are collated, for mean size at breeding and breeding density, values for the two species vary together from year to year. There is no evidence of competition bringing about an inverse relationship between *Lymnaea* size and *Physa* size, or between *Lymnaea* density and *Physa* density, from year to year at the same locality.

The few figures for number of egg-masses per square metre in Table 8 are again, as in *Physa*, approximate, being each a proportionate number allocated to *Lymnaea* of the total egg-masses per square metre. From these samples it is impossible to draw any conclusions regarding the relationship

Table 8—Summary of density data for nine years for breeding *Lymnaea peregra*, Rossdhu "Old" and "New" littoral stations, Loch Lomond.

Year	1949	1950	1951	1952	1953	1954	1955	1956	1956	1957	1957	1958
Station	Old	Old	Old	Old	New	—	New	Old	New	Old	New	Old
No. of adults determined per sq. m.	113*	180*	99*	39*	43	n.r.	36	58	22	112	48	47
Approximate no. of egg-masses per sq. m.	n.r.	n.r.	n.r.	n.r.	n.r.	n.r.	134	n.r.	216	n.r.	391	283

n.r. = no records available.

*Converted from data for migration studies (Hunter, 1953 b).

between adult density in *Lymnaea* and number of egg-masses. Data from other populations of *Lymnaea peregra* living elsewhere in streams in the West of Scotland suggest, however, that the number of eggs produced per adult is proportionately lower at high adult densities, as for *Ancylus*, though not for *Physa*. Over all the samples counted in the littoral zone of Loch Lomond, the numbers of egg-masses per adult *Lymnaea* vary considerably, ranging from three to eleven per adult. Assessing total egg-production per adult *Lymnaea* in these Loch Lomond populations is complicated by the presence of two distinct types of *Lymnaea* egg-masses. Commonest are small egg-masses containing 12 to 15 eggs. Larger ones of 90 to 120 eggs are less common, but may make up a greater proportion of the total *Lymnaea* eggs laid. In 1957, for example, there were three of the smaller egg-masses to each of the larger form. A further difficulty arises from the longer duration of egg-laying in these populations, which may extend from late March until the end of June, with a peak of activity about the first week in June. Probably about one-third of the total egg-production is counted in such " end-of-May " samples. Therefore an individual *Lymnaea peregra* in these populations in Loch Lomond must produce between 315 and 1,155 eggs through the breeding season. Other populations of the same species elsewhere in the West of Scotland produce a less variable and larger number of eggs, and Hunter (1953 a, 1956, 1957) has given as a mean figure, 1,400 eggs per adult. These figures are in reasonable agreement with Boycott (1936 ; see also Boycott, Diver, Garstang & Turner, 1930) who states that some races of *L. peregra* in captivity average about 500 eggs and can produce 3,000, while other races produce about 200 eggs. Bondesen (1950) quotes earlier records of *L. peregra* producing 1,300 eggs per adult per season. It is impossible to decide at present whether these populations in Loch Lomond are in fact a mixture of two distinct races of *Lymnaea peregra*, each with its characteristic type of egg-production. Both types of egg-masses are found elsewhere in the West of Scotland in a variety of habitats, and in a number of other cases together as in the Loch Lomond littoral zone. The two sizes of egg-masses, containing 90 to 120 eggs and 12 to 15 eggs respectively, may correspond to the two types described by Bondesen (1950) as the normal egg-masses with up to 200 eggs, and the " hunger-form " with rarely over 20 eggs. He suggested that the latter were laid by *Lymnaea peregra* living in poor conditions in running water (and perhaps also in brackish water). But, in the West of Scotland, the larger form of egg-masses is commonly found in streams, such as the Upper Craigton Burn. Boycott, Diver, Garstang & Turner (1930) have also described different sizes of egg-masses laid by different populations of *Lymnaea peregra*. The question remains obscure, but probably the size of egg-masses has a partially phenotypic, but also partially genetic, basis.

Annual variation in productivity in *Lymnaea peregra* has been assessed in Table 9 as for the other two species. As for *Physa*, the relationship between volume and shell-length in *L. peregra* can be derived from earlier work (Hunter, 1953 c). A suitable conversion factor for adult *Lymnaea* is 0·1505, which multiplied by the cubes of the mean lengths provides the volume values of Table 9. The bottom line of the Table gives the assessed productivity values

Table 9—Annual variation in mean lengths, calculated volumes, and assessed productivity for breeding *Lymnaea peregra*, Rossdhu littoral stations, Loch Lomond.

Year	1950	1951	1952	1953	1954	1955	1956	1957	1958
Mean length in sample mm.	9·15	7·38	8·75	8·39‡	n.r.	10·13*‡	9·19	10·21†	7·12
Calculated volume cu.mm.	115·29	60·49	100·82	88·88	—	156·45	116·81	160·18	54·32
Assessed productivity cu.mm./sq.m.	20,752	5,989	3,932	9,066	—	13,455	6,775	17,940	2,553

n.r. = no records available.

*Adjusted to end-of-May value, see text.

†" Old " station value see text.

‡Adjusted from " New " to " Old " station values, see text.

for *L. peregra* in the Loch Lomond littoral zone at Rossdhu. They are products of the population density figures for adult snails and the calculated volumes for snails of mean length in each year. They are again comparative values of volume of *Lymnaea*-tissue produced per square metre of the lake shore for each year. Once again they cannot be used as *absolute* measures of productivity because of the several qualifications regarding density asssessments and calculated volumes.

SUMMARY OF WEATHER RECORDS

All data presented here were extracted from records kept by the Parks Department of the Corporation of Glasgow. The writer's thanks are due to Mr G. H. Garside, Director of Parks, for supplying copies of the summarized weather reports for each year, and for allowing access to the more detailed records on several occasions. Variations from year to year in the more significant records are shown in Table 10. Data on hours of bright sunshine and means of daily air temperature maxima and minima for winter months were obtained from records made at Springburn Park, Glasgow. Rainfall figures are from Balloch Park, Loch Lomond, and figures for the number of days of air frost from Queen's Park, Glasgow. The observatory at Springburn Park is approximately seven miles from the Upper Craigton Burn station where the *Ancylus* population was studied ; their heights above sea level 351 feet and 365 feet respectively. The observatory at Balloch Park lies between Craigton Burn and Auchentullich Bay, Rossdhu, Loch Lomond, where *Physa* and *Lymnaea peregra* were studied ; it is nine miles from the former and four miles from the latter locality. These Balloch Park records probably represent an intermediate rainfall condition, there being slightly less rain at Craigton and slightly more at Rossdhu. Unfortunately, the only readily available figures for the number of frosty days in each winter are from Queen's Park, which lies in the south of Glasgow, some ten miles from Craigton and twenty-one miles from Rossdhu, Loch Lomond. However, these figures for the number of days on which 1°F or more of air frost was recorded, are representative of the comparative severity of the winters over the whole Glasgow area.

Data for each year presented in Table 10 are summed so as to correspond to the year immediately preceding each annual sampling, i.e. to include the eleven months or so during which the breeding snails sampled have been growing. Thus, each year's total figures for rainfall and for sunshine hours are from 1st June to the end of May. It should be noted that three years' sunshine records quoted in Hunter (1953 a) for 1948–51 are not comparable with these, since they run from the end of June to the end of June. Separate figures are given for the hours of sunshine in the three months, January to March in each year. In these pre-spring months the amount of sunshine is of course important (Hunter, 1953 a) in controlling the growth of diatoms and filamentous algae which form the basic food of all pulmonate freshwater snails. Figures are also presented separately for rainfall during the four summer months of June to September in each year, during which young spat snails grow most rapidly. Both droughts and excessive spates (with

Table 10—Summary of significant weather records for the years 1948 to 1958

Season	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54	1954–55	1955–56	1956–57	1957–58
*Sunshine hours Jan., Feb. & Mar.	196·7	186·0	136·9	204·3	173·1	165·7	247·0	190·4	142·1	170·7
*Sunshine hours June to May	1160·3	1288·9	1189·7	1193·1	1260·5	1052·9	1208·9	1460·9	1166·2	1216·4
†Number of days with air frost	38	39	73	55	48	35	57	51	23	53
*Mean max. temp. Dec., Jan. & Feb.	7·4	6·3	4·0	5·7	6·3	5·6	5·0	4·9	7·1	5·9
*Mean min. temp. Dec., Jan. & Feb.	2·0	1·1	−0·8	−0·2	1·0	0·7	−0·4	−0·4	1·7	0·4
‡Rainfall, inches June to Sept.	28·02	10·65	28·81	17·33	15·72	18·95	24·26	14·29	22·00	17·29
‡Rainfall, inches June to May	76·25	54·45	61·42	54·30	49·05	63·68	71·99	49·40	61·69	54·05
Breeding stock	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958

*At Springburn Park, Glasgow
†At Queen's Park, Glasgow
‡At Balloch Park, Loch Lomond
} —for further details of localities, see text.

Note : The number of days with frost (third line of Table) is in fact the number of days on which 1°F or more of air frost was recorded at Queen's Park, Glasgow. The means of daily air temperature maxima and minima for the winter months, recorded in Fahrenheit degrees at Springburn Park, Glasgow, appear converted to Centigrade degrees in the fourth and fifth lines of the Table.

high loch water levels) markedly increase the mortality of newly hatched spat and young snails. In Table 10 are also presented the means of daily air temperature maxima and minima (converted to Centigrade degrees) for December to February in each season. These temperature records, with the number of frosty days, allow the relative severity of winters to be compared. From the viewpoint of the snail populations, then, significant weather conditions are the summer's rainfall, the winter's severity and sunshine in the early spring (all summarized in Table 10).

DISCUSSION OF ANNUAL VARIATIONS

In freshwater species of pulmonate snails, the size of breeding adults varies greatly from locality to locality (Hunter, 1953 a, 1957, 1961 ; De Wit, 1955 ; Geldiay, 1956). Similar variation occurs in both size at breeding, and density of breeding populations, from year to year in the same place. Data on annual variation in breeding size in a population of *Ancylus fluviatilis* over four years were discussed by Hunter (1953 a), in which breeding size was (perhaps naïvely) related to the amount of sunshine in early spring in each year. In work on migrations in *Lymnaea peregra* (Hunter, 1953 b), data were presented on annual variations in density in inshore populations of that species in Loch Lomond. The present paper has reported annual variations in size, density and assessed productivity in breeding stocks of *Ancylus*, *Physa* and *Lymnaea peregra*. The data extend over ten years and are complete for five years for *Physa* and for eight years each for *Ancylus* and *L. peregra*. The more significant weather records for the West of Scotland for this period have been summarized above (Table 10).

For ease of comparison the data on size, density and productivity are presented as annual index figures in Table 11, as nine sets : for size, density and assessed productivity in each of the three species. Each set of index figures has been calculated by taking the mean of the mean values for each year as 100. For example, in the case of size in *Ancylus* (at the top of Table 11), the mean lengths range from 5·22 mm. (in 1951) to 6·48 mm. (in 1950), and the mean of these values over nine years is 6·03 mm., which is taken as 100 in the series of index figures. These annual index figures are also represented by the black histograms in the lower part of Fig. 4.

Considering the annual index figures for size in Table 11, those for *Ancylus* range from 87 to 107, for *Physa* from 91 to 107, and for *L. peregra* from 81 to 116. The finding that variation in size is greater in *L. peregra* than in *Physa* and *Ancylus* is not unexpected, and confirms the qualitative impression gained of the three species during more widespread field collecting. *Ancylus* and *Physa* are more uniform, and *Lymnaea peregra* more variable in growth. Populations of *L. peregra* are also more variable in respiratory behaviour (Hunter, 1953 b & c, 1957), in breeding patterns and reproductive rates (Hunter, 1961 and this paper), and in feeding behaviour and food requirements. This species occurs in a far wider range of habitats than either *Ancylus* or *Physa*, and can be considered the most euryoecic of British freshwater gastropods.

Table 11—Variation in size, density and productivity as annual index figures for *Ancylus*, *Physa* and *Lymnaea peregra*.

	Years	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	Means
Ancylus fluviatilis	Mean length mm.	6·19	6·48	5·22	6·07	5·23	n.r.	6·34	6·41	6·03	6·27	6·03 (9 yrs)
	Size indices	103	107	87	101	87	—	105	106	100	104	
	Adult density per sq.m.	n.r.	518	132	324	168	n.r.	392	97	240	212	260 (8 yrs)
	Density indices	—	199	51	125	65	—	151	37	92	82	
	Assessed productivity cu.mm./sq.m.	—	13,670	1,822	7,028	2,332	—	9,690	2,478	5,105	5,069	5,899 (8 yrs)
	Productivity indices	—	232	31	119	40	—	164	42	87	86	
Physa fontinalis	Mean length mm.	n.r.	n.r.	n.r.	n.r.	5·86	n.r.	6·24	6·52	6·61	5·61	6·17 (5 yrs)
	Size indices	—	—	—	—	95	—	101	106	107	91	
	Adult density per sq.m.	n.r.	n.r.	n.r.	n.r.	76	n.r.	81	41	123	62	77 (5 yrs)
	Density indices	—	—	—	—	99	—	105	53	160	81	
	Assessed productivity cu.mm./sq.m.	—	—	—	—	2,034	—	2,618	1,511	4,724	1,456	2,469 (5 yrs)
	Productivity indices	—	—	—	—	82	—	106	61	191	59	
Lymnaea peregra	Mean length mm.	n.r.	9·15	7·38	8·75	8·39	n.r.	10·13	9·19	10·21	7·12	8·79 (8 yrs)
	Size indices	—	104	84	100	95	—	115	105	116	81	
	Adult density per sq.m.	113	180	99	39	102	n.r.	86	58	112	47	93 (9 yrs)
	Density indices	122	194	106	42	110	—	92	62	120	51	
	Assessed productivity cu.mm./sq.m.	—	20,752	5,989	3,932	9,066	—	13,455	6,775	17,940	2,553	10,058 (8 yrs)
	Productivity indices	—	206	60	39	90	—	134	67	178	25	
		1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	

In the index figures for density in Table 11, those for *Ancylus* range from 37 to 199, for *Physa*, from 53 to 160, and for *Lymnaea peregra*, from 42 to 194. Thus the annual variations in density in these relatively stable populations are considerable and can be of the order of : more than five-fold in *Ancylus*, three-fold in *Physa* and nearly five-fold in *Lymnaea peregra*. The population of *Physa* is not necessarily less variable in density than the populations of the other two species. The highest densities recorded for

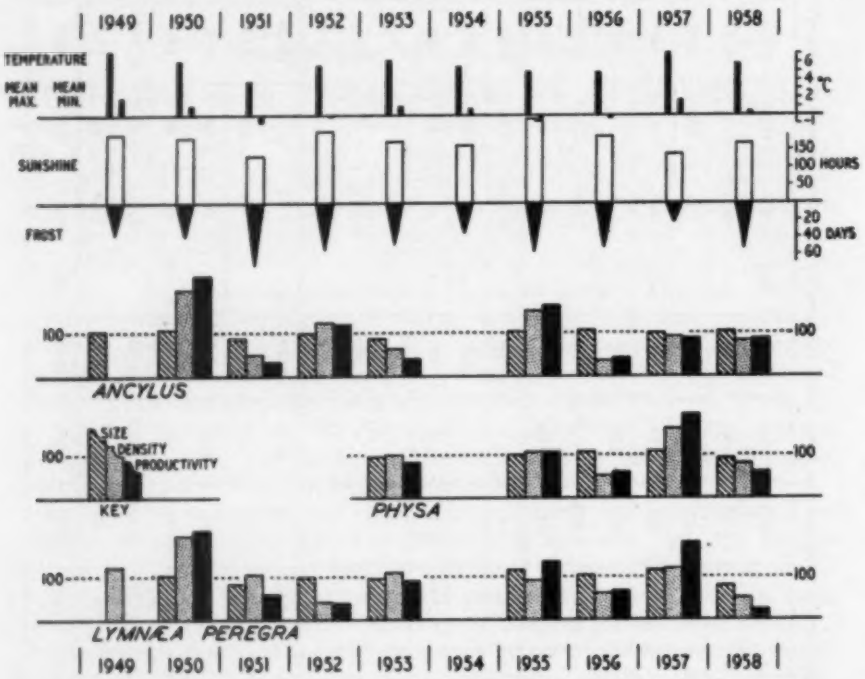

Fig. 4—Overwinter weather, and annual index figures showing variation in size, density and productivity for overwintered breeding stocks of *Ancylus*, *Physa* and *Lymnaea peregra*. The black columns on the upper line show the means of daily air temperature maxima and minima for the months of December, January and February ; the open blocks represent the total number of hours of sunshine during the months of January, February and March ; and the black triangles below them indicate the number of days on which 1°F or more of air frost was recorded. For each of the three species the cross-hatched blocks represent the annual index figures for size ; the dotted blocks those for density, and the black blocks, those for productivity in each year. For further explanation, see Tables 10 and 11 and text.

Ancylus and *Lymnaea peregra* were in 1950, for which no records of *Physa* are available. Index figures for assessed productivity in Table 11 show even greater variation, since density is a factor in each productivity assessment and, as has already been pointed out, there is no indication of any inverse relationship between size and density. Thus, annual variation in assessed productivity

can be over seven-fold in *Ancylus*, more than three-fold in *Physa* and over eight-fold in *Lymnaea peregra*. Such annual fluctuations in molluscan productivity must obviously affect, both directly and indirectly, the food available for fishes—and for other more casual predators such as water-birds.

When these index figures are considered year by year with available weather data (Table 10, see also Fig. 4), a number of features are clearly significant. First, the most severe winter of the series (1951) produced markedly low figures for both *Ancylus* and *Lymnaea peregra*. (No *Physa* records are available for that year.) Secondly, with a few exceptions which will be discussed specifically later, there is a broad, general agreement between the figures for the three species in each year. In more detail, in both *Ancylus* and *Lymnaea peregra*, an extremely productive year in 1950 was followed by an exceedingly poor year in 1951 : and for all three species the years 1955, 1956 and 1957 form a series of good, poor and good years as regards production. Thirdly, annual variations in production in *Ancylus* do seem to be related more closely to spring sunshine than in the other two species. Fourthly, there is very close correspondence between the figures for *Physa* and those for *Lymnaea peregra* in *all* five years for which full data of both are available. Fifthly, the general severity of the winter (measured, for example, by the temperature means from December to February) is the most important factor producing annual variations in production in *Physa* and *Lymnaea peregra*.

The apparent inconsistencies between different species which occur in a few of the years surveyed, arise from the relationships noted above. For example, production was relatively higher in *Ancylus* in 1952 and 1955 than in the other two species in these years. In both cases the growth-year of the snails (i.e. 1951–2 and 1954–55) encompassed a relatively severe winter, combined with relatively high levels of sunshine from January to March. On the other hand, production was relatively lower in *Ancylus* in 1953 and 1957 than in the other two species in these years. These two growth-years, 1952–53 and 1956–57, had relatively mild winters, but with relatively low values for sunshine in the early spring months. This conclusion, that the amount of spring sunshine is of less direct importance to *Physa* and to *Lymnaea peregra* than to *Ancylus* is almost certainly connected with a biological difference between these species in their food requirements and feeding behaviour. In typical highland streams—indeed in all its habitats—*Ancylus* lives on a hard substratum (usually a stone surface), and grazes more or less continually on the attached diatoms and filamentous algae coating it. In contrast, *Lymnaea peregra* lives on a variety of substrata (Hunter, 1953 b, 1957) and can feed on higher plants directly, on organic detritus of all kinds including dead animal tissue, and on suspended micro-organisms on the surface film, as well as on the attached diatoms and other algae of the substrata. For example, the present author has observed, on several occasions in oligotrophic " highland " lochs in Scotland, numbers of *L. peregra* making considerable migrations to feed directly on vertebrate carrion. *Ancylus* is a more limited herbivore, a microphagous " scraper " using the terminology of Yonge (1928, 1954), while *Lymnaea peregra* is unspecialized and omnivorous. In the particular population studied, *Physa* is far from being as specific a

microphage as *Ancylus*, and feeds on organic detritus, and directly on young plants, in addition to diatoms. However, it is probably much less plastic in feeding behaviour than *Lymnaea peregra*, though living in approximately the same habitat with the same availability of food. As Weerekoon (1953, 1956) first pointed out, a major part of the food supply of the littoral benthos in Loch Lomond (including these *Physa* and *L. peregra*) is allochthonous debris derived from the woodlands around the lowland part of the lake. To sum up, the amount of sunshine in the spring months might be expected to have a greater direct effect on the more specific food of *Ancylus* in the shallower, clearer waters of a highland stream.

Rainfall figures have to be considered in the cases of *Physa* and *L. peregra* living in the inshore waters of Loch Lomond. Field observation in late summer and autumn (Hunter, 1953 b, and unpublished work), has shown that both droughts and spates (or any rapid changes in loch water level) markedly increase the mortality of young snails. The summer (post-hatching months of June to September) and annual rainfall figures were given in Table 10. There were five breeding seasons in the series (1950, 1952, 1953, 1956 and 1958) in which the preceding years had had low rainfall. In 1950 and 1953, densities of *L. peregra* and *Physa* were average or above, perhaps as a result of mild weather overwinter. In the other seasons with low rainfall (1952, 1956 and 1958), adult breeding densities of the two species were low. In *L. peregra* particularly, densities and productivity assessments for the years 1952 and 1958 were extremely low.

Fluctuation from year to year in the relative variability of size within each population, not yet considered, is brought out by the columns of standard deviation in Tables 1, 4 and 7, and is obvious in the histograms of Figs 1–3. Noteworthy among the growth samples, as showing great variability in size within the sample, are those of *Ancylus* in 1956, *Physa* in 1957 and 1958, and *Lymnaea peregra* in 1950 and 1956. There is no obvious correlation with any of the other variables. For example, some relationship between this degree of variability and the corresponding population density might have been expected, since many overwinter selection pressures must affect both. But this is not so, nor apparently is variability related to mean size or to overall productivity. The size of breeding *Ancylus* was most variable in the year of lowest density (1956) of that population. Great size variability occurred in *Physa* and in *Lymnaea peregra* in years of greatest population densities (1957 and 1950). Finally, there is no obvious correlation between size variability in any species and any of the summarized weather data.

To examine whether prediction of productivity is possible, the years surveyed from 1949 to 1958 can be ranked by weather conditions from " good " years for snails to " bad " years Thus, the " worst " year for winter weather (1951) clearly resulted in low snail production. The next " bad " year (1955) had compensating, very high sunshine figures, and productivity in *Physa* was average and in *Ancylus* and *L. peregra* well above average. A further " bad " year (1956) had low production in all three species. On the other hand, data are incomplete for the " best " year (1949). The next " best " year (i.e. with mildest winter, etc.) was 1957 which showed high production in

Physa and *L. peregra*, but lower than average figures for *Ancylus* connected with low amounts of sunshine in that spring. A further "good" year (1950) had very high productivity in the two species for which data are available.

It must be admitted that, even after thus considering data covering some nine years for three species, it is not yet possible to predict the productivity of a population at its breeding season from knowledge of the weather conditions during the eleven months or so preceding that breeding season. As discussed above, it is possible in cases of extreme variation in growth, density and productivity to indicate specific climatic causes, especially in cases of unusually low values, related to more severe weather conditions in the preceding winter. In other words, using the sort of data presented here, causal analysis of the variations of snail stocks in nature is possible, but only where there is considerable deviation from average values, especially deviation downward. Prediction of the values for snail stocks is not yet possible, and it is least likely with near-average weather conditions and near-average snail breeding stocks. As this present paper is being completed (summer 1959), the West of Scotland is experiencing its finest summer weather for many decades. It is interesting to speculate on the effects of continually high temperatures, and near drought conditions upon the productivity of freshwater snail populations (and the amount of fish food thus provided) at their breeding season in May/June 1960. A great deal will depend, as the above figures show, upon the severity of the winter of 1959/60.

GENERAL DISCUSSION

In the previous section are discussed the possible relationships between annual variations in the breeding populations of these snails and differing weather conditions. A few more general aspects of the work remain to be considered.

As is true for most freshwater pulmonate snails (Hunter, 1957, 1961), the three species considered here have fundamentally a simple annual life-cycle, i.e., most grow for one year and die after spawning, and there is usually a single "breeding season" in late spring or early summer. This simple cycle is strictly true of the populations of *Ancylus fluviatilis* and *Lymnaea peregra* discussed here. The population of *Physa fontinalis* studied inshore in Loch Lomond shows a small amount of breeding activity in the late summer (Hunter, 1961). Thus some of the snails hatched in early summer have grown and matured so rapidly as to be able to breed themselves before the autumnal fall in water temperatures. The snails which hatch from the eggs laid in this late breeding period amount to only a small fraction (usually less than 8 per cent) of the overwintering stock of *Physa* in this population (Hunter, 1961). Although there can thus be two generations in a year in this population of *Physa*, there is no question of any replacement of one generation by the other. The small numbers of "autumn-born" *Physa* can be distinguished on a basis of shell length in growth samples taken from this population through the winter, but from March onwards it is impossible to separate them from the rest of the population, since the spring growth of these younger snails has allowed them to "catch up" with the majority.

Thus, for the purposes of the present study of variation from year to year in growth, it was necessary to treat the data on *Physa* no differently from those for *Ancylus* and *Lymnaea peregra*.

In an earlier paper on the growth and life-cycle of *Ancylus* (Hunter, 1953 a) reference was made to the erroneous assumption by several earlier authorities that a biennial cycle is general in freshwater pulmonates. It was also noted that surprisingly few field studies on growth and life-cycle in the commoner freshwater molluscs had then been published, and the few thorough field studies, mostly by American workers, were discussed. More recent publications include De Wit's detailed study (1955) of a population of *Physa fontinalis* at Botshol, Utrecht, Holland, in which he found that two generations per year occurred, with complete *replacement* of the spring-born generation by an overwintering generation. In America, De Witt (1954 a, b, c, 1955) has published important studies on growth and life-cycle in *P. gyrina*. These include laboratory studies on growth (De Witt, 1954 a) and of reproductive capacity (De Witt, 1954 b-c), and field studies on life-cycle and general ecology (De Witt, 1955). In the last, De Witt describes a simple annual life-cycle for this species in the field and notes that the breeding season is three to four weeks later in populations living some 300 miles further north. De Witt & Sloan (1958) have also published the results of a laboratory study on reproductive capacity in *Lymnaea columella*. Geldiay (1956) has studied various local populations of *Ancylus* in different habitats in the English Lake District. In most typical populations (i.e. in highland streams), Geldiay independently confirmed the pattern of growth and life-cycle described for this species by Hunter (1953 a) in the West of Scotland. In the Lake District, however, Geldiay (1956) found some variation from locality to locality in the months in which the maximum size was reached, and also when breeding began, and in one instance he had evidence of breeding recurring in late summer. This " second generation " was of the type mentioned for *Physa* in Loch Lomond above (see detailed account in Hunter, 1961), and merely made up a small part of the overwintering stock—there being no " replacement ". In a lochan at an altitude of 1,450 feet, on the Isle of Skye, Scotland, the breeding season of *Ancylus* appears to be about nine weeks later than at sea level (Hunter & Hunter, 1956). Finally, the study (Hunter, 1961) already mentioned has been prepared on variations in growth and reproductive cycles in different populations of the same species in different habitats. This work on infraspecific variation covers four species : the pulmonate snails, *Planorbis albus*, *Physa fontinalis* and *Lymnaea peregra* and the prosobranch (" operculate ") snail *Valvata piscinalis* ; all in limited populations in Loch Lomond and elsewhere. Samples compared were from contemporaneous collections (mainly collected over the seasons 1952–54) and thus the infraspecific inter-population variations were not obscured by year to year variations of the sort described in this paper. Much inter-population variation occurs within each species in seasonal patterns of growth, in overall growth rates and in time and intensity of breeding. In a few cases, these can be related (Hunter, 1961) to differences in food available for the populations, and in water temperatures to which they are exposed. In general, the onset of the breeding season in

these snails, and therefore, the type of annual cycle which occurs, is dependent both on external factors, of which water temperature is by far the most important, and also on causes endogenous to the snails. The latter may involve the summed effects of the temperatures and trophic conditions experienced by each snail during its growth from hatching to sexual maturity, but is not entirely separable from growth as there is a definite minimum breeding size for each species. In extreme cases the onset of breeding is determined either by environmental temperature alone, or by size and endogenous factors alone (Hunter, 1961). Thus, in several populations of *Lymnaea peregra*, the overwintering stock is mostly above the minimum breeding size for the species with apparently mature reproductive organs, and therefore egg-masses are produced when the water temperatures rise above 9°C in late spring. On the other hand, in a population of *Planorbis albus* living offshore in Loch Lomond at the rise in water temperatures in spring the snails are all below minimum breeding size with little development of the female reproductive system, so that egg-production in this population does not occur until mid- or late-July, after a considerable period of summer growth. It is not unlikely that both external temperatures and endogenous factors could affect the life-cycle by a hormonal mechanism. This might involve a substance like diantalin, whose action on spawning in oysters has been known for some time (Nelson, 1936 ; Nelson & Allison, 1940), or depend on a neurosecretory mechanism such as Lubet (1955, 1956) has recently shown to affect spawning in the marine bivalves, *Mytilus* and *Chlamys*. Direct, short-term effects, and indirect effects (over the whole annual cycle), of environmental temperatures on reproduction have been more extensively studied in marine animals : e.g., Barnes (1958) and Barnes & Barnes (1959) on barnacles, Loosanoff & Nomejko (1951) and Thompson (1958) on molluscs, Millar (1958) on ascidians, and references to earlier work in Hutchins (1947).

As well as the breeding season, the factors determining adult mortality will be affected, by inter-population and by annual variations in growth and density. In most known life-cycles for annual species of freshwater pulmonates, the adults die soon after breeding. In these species growth seems to be still continuing when death occurs (Van Cleave, 1935 ; Hunter, 1953 a, 1957, 1961 ; De Wit, 1955 ; De Witt, 1955 ; Geldiay, 1956). As Van Cleave (1934, 1935) first discussed, growth in many molluscs, in contrast to the process normal in arthropods and in vertebrates, is usually continuous throughout life without cessation at maturity. Hunter (1953 a) suggested that in typical " highland stream " populations of *Ancylus* there is environmental limitation of growth (and therefore of age), dependent on the rate of water flow and the growth of algae attached to the shell. Certainly, in typical populations of *Ancylus*, like that studied here, it appears that individual limpets do not survive after they have attained a critical size. It is likely that there is a similar critical size, above which adult death is more likely, in the populations of both *Physa* and *Lymnaea peregra* studied in the littoral at Loch Lomond. The environmental selection there may work through the respiratory needs of the snails in the higher water temperatures of summer. Figures are given elsewhere (Hunter, 1953 c) for the proportionate decrease with growth in,

the surfaces available for cutaneous respiration in both these species. In addition work on migrations in *L. peregra* (Hunter, 1953 b) showed that under certain conditions, the larger adult snails were more liable to a degree of starvation than snails of a few weeks old in the same population. This does not necessarily conflict with the occurrence to some extent of " endogenous senescence " (in the sense used by Comfort, 1956, 1957)—but the fact that " environmental limitation " appears to be less effective in less normal habitats merely emphasizes the importance of attaining a critical size in the usual environments of these snail species in nature. The selective advantages of an annual cycle in which the adults do not survive long after breeding to compete for food with their offspring, are obvious. In the three species discussed here, considerable annual variation occurs in the densities of, and the size attained by, the snails at their breeding time. An environmental cause of death at a critical size, combined with the plasticity of reproductive behaviour in these snails (Hunter 1961, and this paper), could also confer selective advantages in maintaining a population of stable size by compensating for the annual variations which occur. Unfortunately, there are no field data on variations in the length of the breeding season to confirm part of this hypothesis. If this compensatory regulation of the population does occur, one would expect breeding to continue longer in years when adult snails were smaller at the onset of the breeding season. It is clear that in *Ancylus* in the Upper Craigton Burn, and *Lymnaea peregra* in the Loch Lomond littoral, there is discriminative selection of the larger adult snails in early summer (Hunter, 1953 a-b, and unpublished work), but there are no assessments available of total egg-production in different years sufficiently accurate to gauge the effects of this.

When the incidence of mortality throughout the life-history, or the " survivorship ", is considered from the available field studies of freshwater pulmonates (Van Cleave, 1935 ; De Wit, 1955 ; De Witt, 1955 ; Geldiay, 1956 ; Hunter, 1953 a-b, 1957, 1961), a relatively high mortality in very young spat appears common to all species. That is : the survivorship curve (see Pearl & Miner, 1935 ; Deevey, 1947) for all these freshwater pulmonates has a pronounced initial dip, and thus approximates to Pearl & Miner's theoretical curve termed type III by Deevey (1947). The potential maximum life span which is probably controlled by internal factors of senescence in Comfort's sense, must be distinguished from actual mean life span in each species/population under natural conditions in the wild. This actual life span is not controlled by endogenous senescence but by environmental limitation. It is worth emphasizing here that discussion of life-cycle and fecundity in these pulmonate snails must be based on field studies on natural populations, particularly if any conclusions on rates of selection are to be drawn.

When the present paper, and that on inter-population variations (Hunter, 1961), were being completed, the important work of Duncan (1959) on the life-cycle of *Physa fontinalis* became available. It was largely based on material from a pond at Stanmore, Middlesex, and from Windermere, in the English Lake District, and the data presented do not conflict with the general

conclusions on variation in growth and reproduction discussed above. In addition, Duncan provides a behavioural analysis of the stimuli which initiate copulation and oviposition in *Physa*. In this, his conclusions independently strengthen the concept outlined above (and in Hunter, 1961) that the onset of the breeding season is dependent on the interaction of endogenous and external factors.

Certain evolutionary considerations follow, and it should again be stressed that the three species/populations for which data on annual variations have been presented are relatively stable populations living in "good" habitats of considerable permanence. Most freshwater snails occur in bodies of water which are both more variable in extent, and more transitory. A medium-sized highland stream with a reasonably steady flow of water throughout the year, and the inshore waters of a very large lake, both present freshwater habitats of *unusual permanence* in both space and time. In less permanent habitats variations in growth and density from year to year can be much greater. Hubendick (1952, 1954) and Hunter (1952, 1956, 1957) have pointed out independently, and from different bases, that the process of evolution in molluscs living in fresh waters has been markedly different from evolution in similar animals living in the sea or on land, largely as a result of the high degree of small-scale, short-term isolation which can occur in freshwater environments. The great plasticity of respiratory behaviour in freshwater snails has been discussed elsewhere (Hunter, 1953 c, 1957), and it appears that there is a similar plasticity in growth cycles and reproductive behaviour. It is suggested that such adaptive plasticity, in respiration, reproduction and in other aspects of the physiology of freshwater snails, is of fundamental selective value. That is, what appears to have been selected *for* in freshwater pulmonates is the capacity to vary—the possession of adaptive plasticity.

Finally, apart from the fundamental significance of these annual variations, certain applied aspects can be mentioned. First, variations in the productivity of snail populations will obviously produce variations in their efficiency as vectors for trematode parasites such as schistosomes. Little has been done on the bionomics of parasite "turn-over" in relation to variations in density and productivity of the snail hosts. However, annual variations in productivity of the order recorded here, could certainly affect the incidence of schistosome dermatitis ("swimmers' itch") at those lakes in North America where the biology of the snail hosts has been investigated (Brackett, 1940; Cort *et al.*, 1940). Secondly, it was suggested in an earlier paper (Hunter, 1953 a) that the growth of ancylids and other molluscs could be used to assess total productivity of fresh waters. Several investigators, notably Baker (1918) and Neill (1938), have studied productivity of freshwater faunas in relation to the feeding of fishes. Reliable quantitative estimations of the whole bottom fauna, particularly on stony substrata, are difficult (see Jones, 1941; Jonasson, 1948; Badcock, 1949; Macan, 1958; and references therein). Assessments of annual and other fluctuations in biomass might well be more reliable if based on studies of a limited number of "indicator-species". However, little use has been made in fresh water of such measurements of growth and density as the present paper provides for three gastropods. In

any body of fresh water, the basic autochthonous food supply is of two sorts : the benthic diatoms and other attached algae, and the nannoplankton in its broadest sense. Measurement of variations in size and density in populations of suitable snails (*Ancylus* in almost all habitats, *Physa* in many) could provide an assessment of annual variations in the benthic primary production. Similar measurement of annual species of filter-feeders, such as *Sphaerium* spp. or certain larger *Pisidium* spp. (e.g. *P. amnicum* or *P. henslowanum*) could assess primary production of phytoplankton. Assessment of variation in productivity in those bodies of fresh water, where allochthonous organic detritus makes up a larger part of the basic food supply, presents further difficulties. Measurements of growth and density in a snail like *Lymnaea peregra*, or in a crustacean like *Asellus aquaticus*, could often provide an assessment of any annual variations in the importance of such allochthonous food. Assessments of growth, density and productivity are best taken from species with simple annual life-cycles, and are best made near the end of each cycle. Theoretically, pluriennial species where growth-rings can be measured could also be used to indicate annual variations in productivity but although attempted in some fishes this method has never been applied to the larger freshwater bivalves.

As admitted above, it is not yet possible to predict annual variations in productivity from the weather records, except in extreme cases. This would seem to strengthen the case for the use of indicator species in a sort of " biological assay " of the year's productivity. Assessed together, records from populations of snail species feeding by radula-grazing on benthic algae, of phytoplankton-feeding bivalves, and of " detritus-feeding " species, might together provide a useful measure of the annual variations in total productivity in a body of fresh water.

SUMMARY

Within any relatively stable population of freshwater snails the average size, and the population density, of adults at the breeding season, both vary from year to year. Data are presented from the West of Scotland covering nine years for populations of *Ancylus fluviatilis* and *Lymnaea peregra*, and five years for a population of *Physa fontinalis*. These populations all have basically simple annual life-cycles. Annual variation in mean size at breeding is about twice as great in *Lymnaea peregra* (i.e. approximately $\pm 17{\cdot}5$ per cent) as in the other two species. Annual fluctuations in adult population densities at breeding can be five-fold in *Ancylus* and *Lymnaea peregra* and three-fold in *Physa*. Assessments of annual productivity for each species have been made, corresponding to volumes of molluscan tissue per unit area (of stream or of lake bottom). Annual variation on assessed productivity can be over seven-fold in *Ancylus*, more than three-fold in *Physa*, and over eight fold in *Lymnaea peregra*.

With certain exceptions, there is broad general agreement between the annual figures for the different species—a year usually being " good " or " bad " for all three—and the annual variations can be correlated with certain of the weather conditions prevailing during the year before each breeding

season. In cases where there is considerable deviation from average values for growth, population density and productivity, it is possible to indicate specific climatic causes with a fair degree of certainty. The severity of the winter seems to be the most important aspect of the year's weather as regards these molluscan fluctuations, particularly in the populations of *Physa* and *Lymnaea peregra*. Annual variations in *Ancylus* seem to be more closely related to spring sunshine, and a possible trophic basis is suggested for this difference between the species. Low rainfall in late summer may also affect adversely the population densities of *Physa* and of *Lymnaea peregra* in the following year. Prediction of molluscan productivity from weather records is not yet possible, and is least likely to become so in years with near average weather conditions.

The relation of this work to other studies on growth and life-cycles in freshwater snails is discussed, with reference to variations in breeding periods and adult mortality. The interaction of external and endogenous factors in controlling life-cycles is briefly considered, and it is advanced as a hypothesis that the great plasticity in growth cycles and reproductive behaviour shown by freshwater snails is of fundamental selective value. The probable significance of such annual fluctuations of molluscan productivity in populations acting as vectors of schistosomes is indicated. Finally, similiar measurements of variations in growth and density in different molluscan populations are proposed as possible means for the assessment of annual variations in the total organic productivity of bodies of fresh water.

ACKNOWLEDGMENTS

Once again I must record my sincere thanks to Professor C. M. Yonge, C.B.E., F.R.S. and to Dr H. D. Slack, F.R.S.E. for their continued encouragement. I am also indebted to Dr J. D. Robertson, F.R.S.E. for kindly reading the manuscript, and to my wife, for assistance both in the field and in the preparation of this paper.

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A NOTE ON THE GROWTH STAGES AND STRUCTURE OF THE ADULT LOPHOPHORE OF THE BRACHIOPOD *TEREBRATELLA* (*WALTONIA*) *INCONSPICUA* (G. B. SOWERBY)

BY

D. ATKINS, D.Sc.

From the Marine Biological Laboratory, Plymouth

[Accepted 11th October, 1960]

(With 10 figures in the text)

Certain of the growth stages of the lophophore of *Terebratella* (*Waltonia*) *inconspicua* (Sowerby), from a shell length of 0·55 mm., are described and figured, so as to elucidate the position of the mouth and the mode of development of the lip of the food groove. The mouth is a small aperture in front of the bases of the first formed pair of filaments. The lip of the food groove is formed by lateral growth from a small preoral lobe. The early lophophore (trocholophous and early schizolophous) is of the broad-based terebratellacean type set low on the dorsal mantle, and the filaments when extended in feeding are directed anteriorly and ventrally. The structure of the adult lophophore is described. The ciliary feeding mechanism is essentially similar to that described by the author in *Macandrevia cranium* (Müller) and other brachiopods with plectolophous lophophores.

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INTRODUCTION

Specimens of the New Zealand brachiopod *Terebratella* (*Waltonia*) *inconspicua* (Sowerby)* were sent to me by the late Professor E. Percival for a study of its ciliary feeding mechanism. Small individuals survived the air journey better than did adults and in examining them I was led to a study of the growth stages of the lophophore. My conclusions concerning the position of the mouth and the development of the lip of the food groove differed from those of Percival (1944). I wrote to him about this fully in 1956. He did not, however, go into these differences in later correspondence with me. Professor C. F. Pantin F.R.S. has kindly let me see—after the original had gone to press—a copy of the typescript of Percival's (1960) posthumous paper on the life-history of the rhynchonellid, *Tegulorhynchia nigricans* (Sowerby), and it is clear that Percival considered that the mode of formation of the lip of the food groove differed considerably from that in *Terebratella inconspicua*, and that he had not changed his opinion as to its formation in the latter. The following account of the formation of the lip of the food groove of *T.*

*For the use of *Waltonia* see R. S. Allan. In Report of the Sixth Science Congress. *Trans. Roy. Soc. N.Z.* **77** pt. 5 : 288–9 (1949).

inconspicua from a shell length of 0·55 m., and my previous accounts of lip formation in certain other brachiopods, are in agreement with Percival's (1960) description of its formation in *Tegulorhynchia nigricans* in that in all the lip originates from an unpaired lobe.

The development of the brachial support of *Terebratella inconspicua* has been described by Thomson (1915, 1927). The usual growth stages of the lophophore are passed through culminating in the plectolophous : these have been figured in contracted state by Percival (1944) to a shell length of about 0·8 mm., and by Elliott (1948, 1954) from a shell length of 1 to 6·5 mm.

A few growth stages of the lophophore are described and figured here to attempt to clear up the existing misconceptions as to the position of the mouth in young stages, the formation of the lip of the food groove, and the normal appearance of the trocholophous and early schizolophous stages of the lophophore when the filaments are extended in feeding.

According to Percival (1944) the mouth in the trocholophous stage of *Terebratella inconspicua* is the circular area surrounded by filaments ; this he showed in his figure 29, plate 5. In his two previous figures, 27 and 28, he showed a circular band or ridge with filaments arising from it. The anterior edge of the band he identified as "edge of mouth". It appears probable, taking into consideration his incorrect identification of the mouth in his fig. 29, that the band is the circular base of the lophophore. As Percival's figures appear to be somewhat diagrammatic, it is possible that the part of the base shown undifferentiated did in fact have rudiments of filaments. If my interpretation of Percival's figures is correct, then it would appear that the lophophore base is a complete circle in its early post-larval state at a length of about 0·2 mm.

Beecher's (1897) taxolophous stage preceding the trocholophous, seems to have been founded on an error. He showed the bow or crescent incomplete posteriorly. No doubt the first-formed pair of filaments were obscured by the thickness of the gut, for in his (1895) work on *Terebratella obsoleta* Dall in which he first showed this stage, he was dealing with material which had been dried and then soaked, and it is surprising that his figures are so good. This omission of posterior filaments is also seen in Kovalevsky's (1874) figures of the early lophophore of *Argyrotheca*, reproduced by Oehlert & Deniker (1883) as their figures 11 and 13. In the former one pair and in the latter two pairs of posterior filaments are omitted. There is actually no posterior gap in the trocholophous lophophore in *Argyrotheca* (see Atkins, 1960).

With regard to the formation of the lip of the food groove in the trocholophe of *Terebratella inconspicua*, Percival (1944) wrote that " at a time when eight pairs of filaments are formed, there is a rapid extension of the anterior border of the mouth, between the latest filaments, without a corresponding increase in the diameter of the opening. The extra margin is accommodated by its bending inward so as partially to close the mouth by forming a crescentic slit with the filaments only on the lateral and posterior border : the anterior invaginated border is always devoid of filaments, no matter how complicatedly folded the mouth becomes, and the addition of new filaments is at the end of each horn of the original crescent distally to those already formed and

alternately on each side as described. The change in shape of the mouth from a circle to an elongated slit makes possible an increase in the number of filaments and in food intake capacity without any other great increase in size of the animal ".

Williams (1956) agreed with this account, for he stated " sections and mounts of rhynchonelloids and other terebratuloids almost as young as the trocholophous *Terebratella* described by Percival suggest that in all articulate brachiopods at least there is no significant variation from this pattern of development and it seems safe to assume that the brachial fold was always formed in the manner described ".

My interpretation from a study of the growth stages of the lophophore of a number of articulates, including *Terebratella inconspicua*, and a rhynchonellid (Atkins, 1959 a, b, c ; 1960 and unpublished work), in which sufficiently young stages were seen, is that the mouth is a small aperture in front of the base of the first-formed pair of filaments and that formation of the lip is by lateral growth of a small preoral lobe, running concentric to the bases of the filaments. My work was done on both living and preserved specimens. The latter were examined either unstained in formalin or alcohol, or stained and in cedar wood oil: they were not viewed as mounts as were those of Percival and Williams. Such procedure would tend to flatten animals of the size of the trocholophous and early schizolophous stages of *T. inconspicua* and to over-clear them, so that distinguising the different layers of tissue would be difficult.

All figures were drawn with the aid of a camera lucida.

GROWTH STAGES OF THE LOPHOPHORE AND LOOP

Some overlapping of the growth stages occurs, the development of the lophophore being more advanced in some animals than in others of the same size. Thomson (1915) remarked that in the young of *T. inconspicua* there is a great deal of latitude in the relations between size of shells and stage of loop-development attained.

T. inconspicua of shell lengths 0·9, 1·5, 1·7, 2·3 and 3·6 mm. have been sectioned transversely. The sections show that by the forward extension and thickening of the body and the growth of the septum, the lophophore is gradually raised above the valve floor.

At a shell length of 0·55 mm. the trocholophe, of the broad-based terebratellacean type set low on the dorsal mantle, has five pairs of filaments, the last pair being short. This stage, shown in Fig. 1A, was drawn from a preserved specimen and so unfortunately the lophophore is somewhat contracted : the filaments are directed anteriorly and ventrally. In front of the mouth is a small lobe, the rudiment of the brachial fold or lip of the food groove, well shown in Percival's (1944) figures 30 and 31, plate 5.

At a shell length of 0·78 mm. seven filaments are present on the left and eight on the right ; the lophophore is still trocholophous. The preoral lobe has extended laterally as a lip, running concentric to the bases of the filaments, and now reaches to the bases of the third or fourth pairs. Figure 1B and C, are of this stage and show the lophophore fairly well extended.

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A specimen of *T. inconspicua* of slightly greater shell length, 0·9 mm., was sectioned. The lophophore was still trocholophous with eight filaments on the left and nine on the right : the lip now extended to the base of the

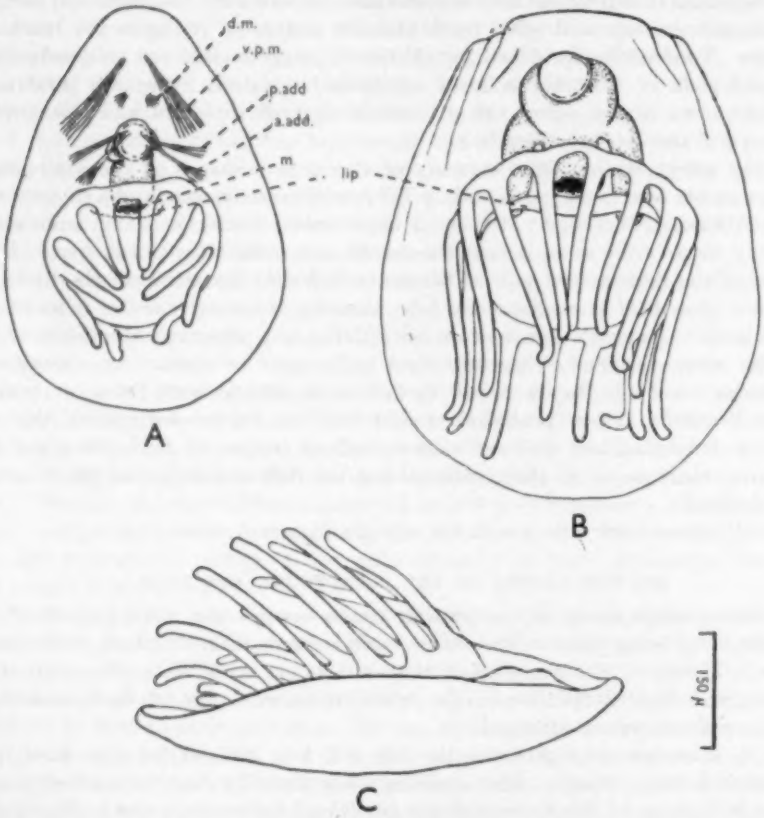


Fig. 1—*Terebratella inconspicua*. A. Entire animal of shell length 0·55 mm., viewed ventrally to show the trocholophous lophophore with five pairs of filaments directed anteriorly and ventrally. Stained with eosin and drawn while in cedar wood oil. B and C. Brachial valve and trocholophe of specimen of shell length 0·78 mm., drawn living ; B. ventral and C. side view.
a. add., anterior adductor muscle ; *d.m.*, diductor muscle ; *lip*, lip of food groove ; *m.*, mouth ; *p. add.*, posterior adductor muscle ; *v.p.m.*, ventral pedicle muscle. The dorsal pedicle muscle is omitted. The mantle setae are omitted.

fifth filament on the right, but not quite as far on the left. It is evident from these sections (Fig. 2) that behind the mouth the filaments arise from the body (Fig. 2A), but that laterally and anteriorly they are set low on the mantle (Fig. 2B-F). The position of the mouth with regard to the brachial membrane (*b.m.*) and the bases of the filaments is shown in Fig. 2B. The mouth is a small aperture opening into the food groove. Fig. 2C passes

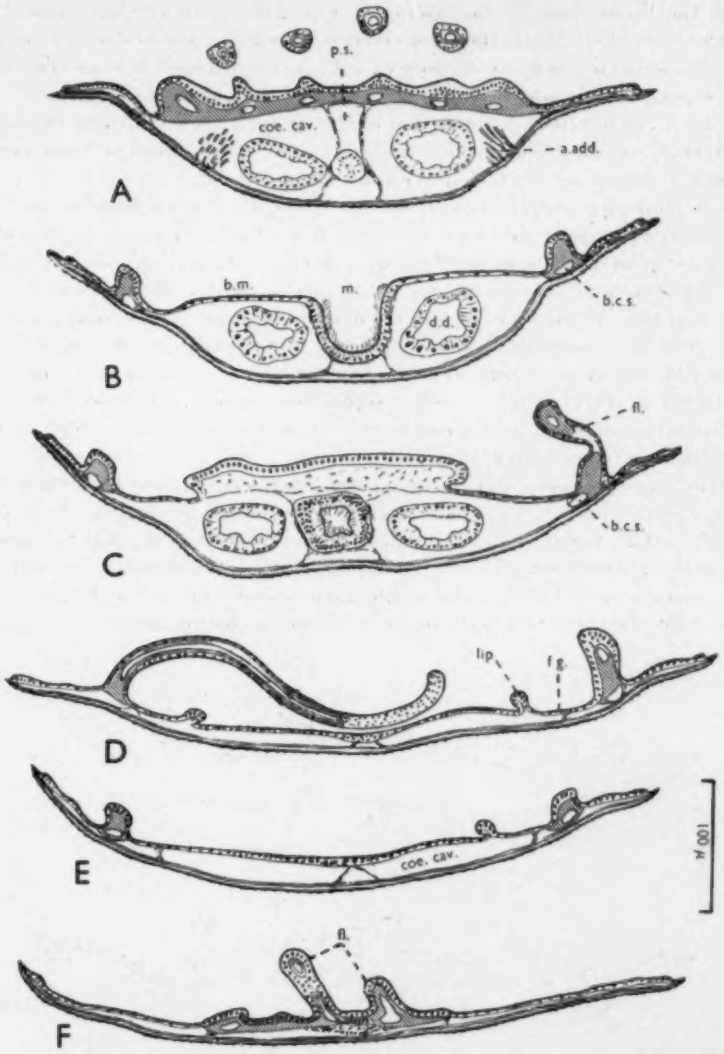


Fig. 2—*Terebratella inconspicua* of shell length 0·9 mm. : lophophore trocholophous. Transverse sections of the brachial valve to show the relation of the lophophore to the mouth, to the lip of the food groove and to the mantle. (A.) through the posterior edge of the lophophore, (B.) through the mouth (*m.*), (C.) through the lip in front of the mouth, (D.) showing the lip of the food groove present on both sides, (E.) section slightly anterior to D, with the lip present on one side only, (F.) through the anterior edge of the lophophore.

a. add., anterior adductor muscle ; *b.c.s.*, small brachial canal ; *b.m.*, brachial membrane ; *coe. cav.*, coelomic cavity ; *d.d.*, digestive diverticulum ; *f.g.*, food groove ; *fl.*, filament ; *lip*, lip of the food groove ; *m.*, mouth ; *p.s.*, pericesophageal sinus. Supporting substance diagonally hatched ; shell substance stippled.

through the lip in front of the mouth. Fig. 2D shows the lip present on both sides, but some 20μ further forward it is present on one side only (Fig. 2E) and in the following sections is absent. A section through the anterior edge of the lophophore is illustrated in Fig. 2F. From these sections and from others it is evident that the formation of the lip is by lateral growth of a small preoral lobe, running concentric to the bases of the filaments, and not as described by Percival (1944) and Williams (1956).

The lophophore remains trocholophous to the time when nine or ten pairs of filaments are present and to a shell length of about 1·5 mm. At this stage the forward growth of the lip of the food groove has caught up with the growth of the filaments and has reached the bases of the last formed filaments.

Interruption of the base of the circular lophophore in the mid-line, with two distinct but contiguous growth zones occurs when some eleven or twelve pairs of filaments are present and at a shell length of at least 1·2 mm. The invagination is of the slightest and the septal boss minute. Differentiation into a double series of inner and outer filaments begins when some eight or nine pairs of filaments are present.

Sections of specimens of 1·5 and 1·7 mm. shell length show the twin growth regions raised above the valve floor by increase in height of the septum (Fig. 3A). The lophophoral ridge runs obliquely up the septum : a section through the anterior edge of the lophophore (Fig. 3B) shows it at the base of the septum raised above the valve floor merely by the coelomic cavity. At this stage the great brachial canal (*b.c.g.*) can be distinguished.

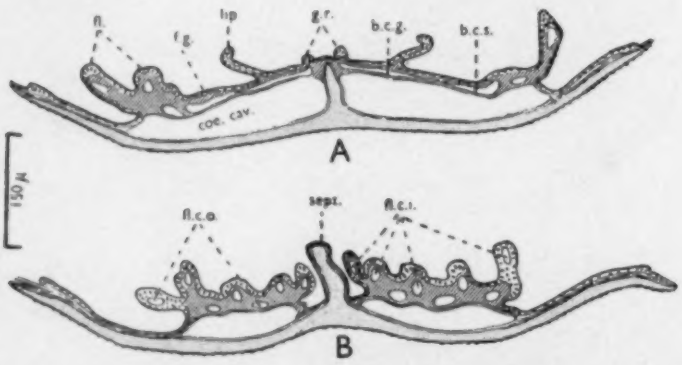


Fig. 3—*Terebratella inconspicua* of shell length 1·5 mm. : lophophore early schizolophous. Transverse sections through the brachial valve to show the relation of the lophophore to the septum and to the coelomic cavity. (A.) through the twin growth regions ; (B.) through the anterior region of the lophophore.
b.c.g., great brachial canal ; *fl.c.i.*, inner and *fl.c.o.*, outer filamentar canals ; *g.r.*, twin growth regions ; *sept.*, septum. Other lettering as in Fig. 2. Supporting substance diagonally hatched ; shell substance stippled.

With growth the invagination of the lophophore in the mid-anterior region deepens and the septum increases in size. A schizolophe with twenty to

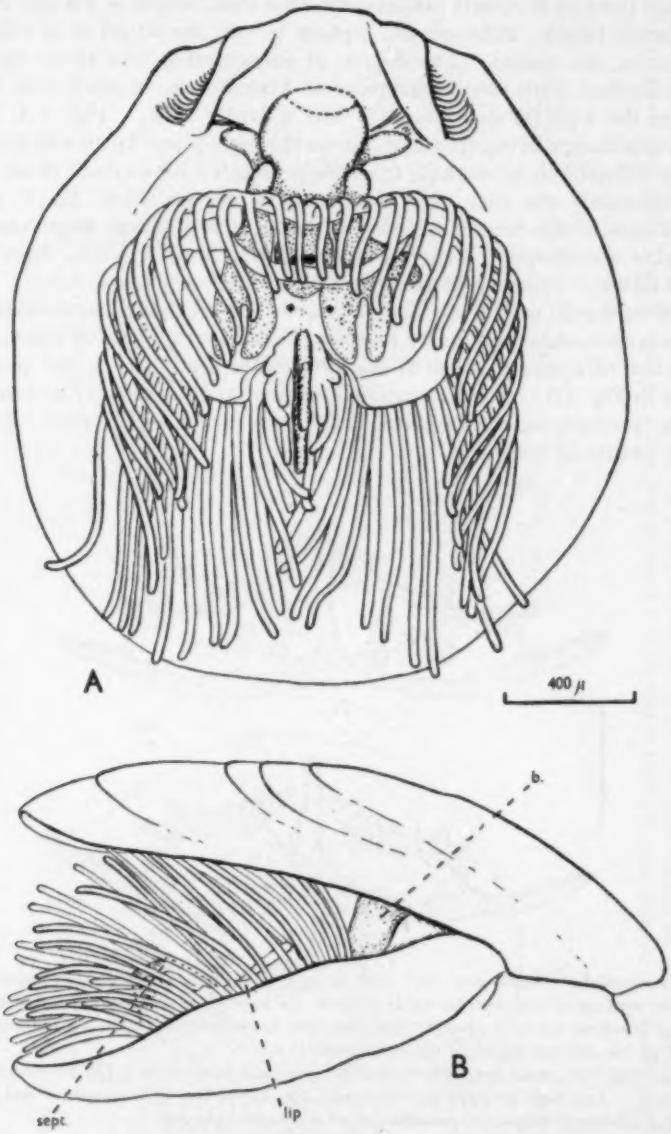


Fig. 4—*Terebratella inconspicua*. (A.) brachial valve with schizolophe of specimen of shell length 2·4 mm., drawn living. The posterior filaments appear short as they are directed ventrally and so are foreshortened. The lip of the food groove is turned outwards in front of the mouth, which is thus exposed. The intestine has been removed. (B.) lateral view of a preserved specimen of shell length 2·0 mm., with the filaments curved slightly inwards.
b., body ; *lip*, lip of the food groove ; *sept.*, septum.

twenty-six pairs of filaments occurs between a shell length of 1·9 and 2·9 mm At the latter length, although the septum is well developed it is without a hood : crura are absent. The degree of invagination was about the same in the individual with twenty-six pairs of filaments as in that with twenty pairs, but the lophophore necessarily had a larger base. Fig. 4 A of this stage, drawn from a living specimen, shows the lophophore fairly well expanded and very different in appearance from the contracted lophophore of an animal of approximately the same size illustrated by Elliott (1954, fig. 7, pl. 16). The filaments of the trocholophous and early schizolophous stages cannot be described as centripetal in *Terebratella*, any more than in *Platidia*, *Macandrevia cranium* (Müller) or in *Terebratalia transversa* (Sowerby) (see Atkins, 1959 a, b, c), and so should not be used as a character distinguishing terebratellaceans from terebratulaceans as done by Beecher (1893) and repeated by later authors. A side view of a similar stage to that illustrated in Fig. 4 A, but preserved, is shown in Fig. 4 B. The two carmine pigment spots, probably in connection with the preoesophageal ganglion are shown in Fig. 4 A : they have been found to persist in adults.

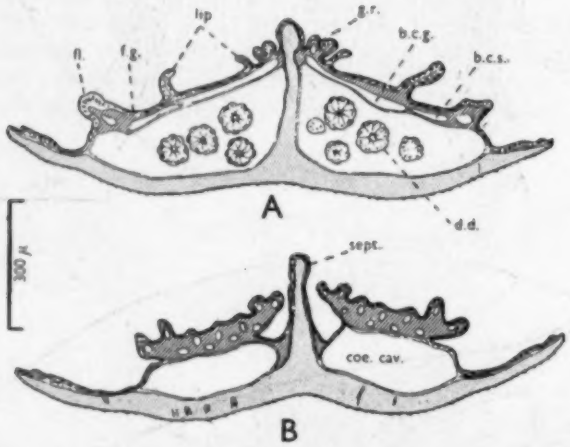


Fig. 5—*Terebratella inconspicua* of shell length 2·3 mm. ; lophophore schizolophous. Transverse sections of the brachial valve to show the relation of the lophophore to the septum and to the coelomic cavity. (A.) through the twin growth regions (*g.r.*) of the lophophore ; (B.) through the anterior region of the lophophore.
b.c.g., great and *b.c.s.*, small brachial canals ; *coe. cav.*, coelomic cavity ; *d.d.*, tubule of digestive diverticulum ; *f.g.*, food groove ; *fl.*, filament ; *lip*, lip of the food groove ; *sept.*, septum. Supporting substance diagonally hatched ; shell substance stippled.

A *T. inconspicua* of shell length 2·3 mm., and of about the same stage as that shown in Figure 4 A, was sectioned. Two sections from this series are illustrated (Fig. 5) ; they show increase in height of the septum, carrying with it the twin growth regions of the lophophore. The coelomic cavity has increased in size and the digestive diverticula extend further forward.

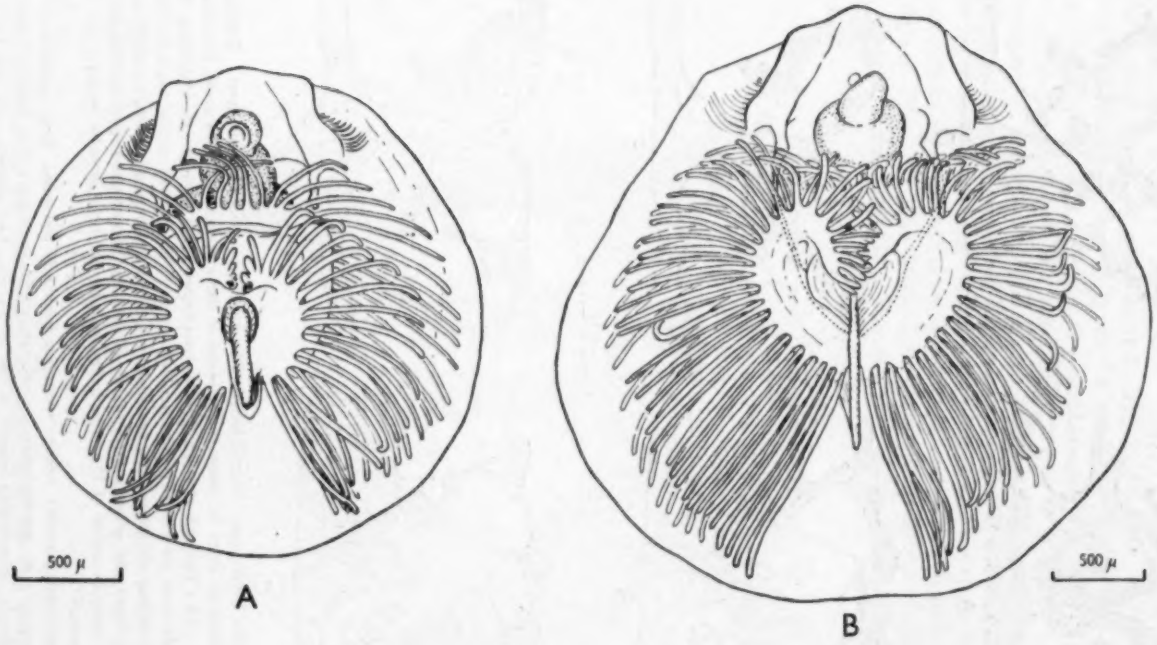


Fig. 6—*Terebratella inconspicua*. A. Brachial valve and early zygolophe of specimen of shell length 2·8 mm. A small fragile hood is present on the posterior region of the septum : crura are present, and on the left the descending branch has begun to grow. B. Brachial valve with late zygolophe of specimen of shell length 4·0 mm. : descending branches complete. Both drawn preserved in formalin, then cleared in cedar wood oil to reveal the brachial support.

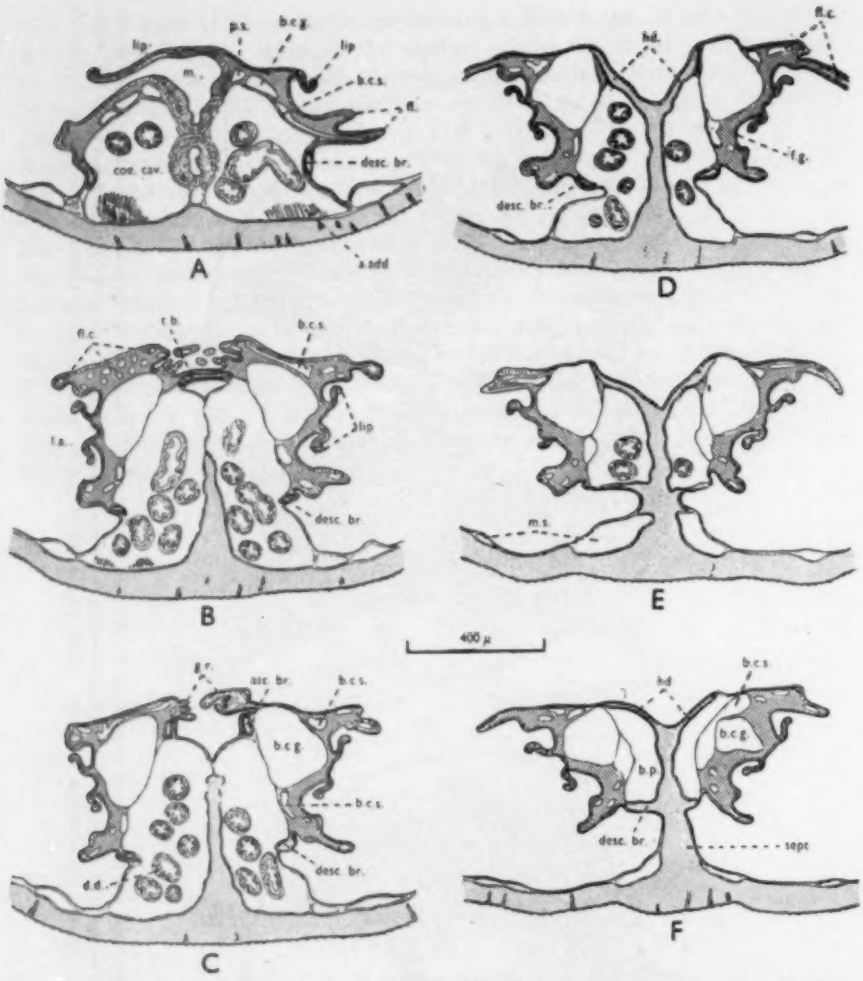


Fig. 7—*Terebratella inconspicua* of shell length 3·6 mm. : lophophore zygolophous. Transverse sections of the brachial valve to show the relation of the lophophore to the loop, septum and coelomic cavity. (A.) through the mouth and oesophagus ; (B.) through the transverse band of the loop and the twin growth regions of the lophophore ; (C.) in front of the transverse band, showing both ascending and descending branches; (D.) through the posterior region of the hood; (E.) through the hood and anterior part of the descending branches arising from the septum; (F.) through the anterior region of the hood to show on the right the anterior recurvature of the small brachial canal.

a.add., anterior adductor muscle ; *asc.br.*, ascending branch of the loop ; *b.c.g.*, great and *b.c.s.*, small brachial canals ; *b.p.*, brachial pouch ; *coe. cav.*, coelomic cavity ; *d.d.*, tubule of digestive diverticulum ; *desc.br.*, descending branch of the loop ; *f.g.*, food groove ; *fl.*, filament ; *fl.c.*, filamentar canal ; *g.r.*, twin growth regions ; *hd.*, hood ; *l.a.*, lateral arm ; *lip*, lip of the food groove ; *m.*, mouth ; *m.s.*, mantle sinus ; *p.s.*, periocsophageal sinus ; *sept.*, septum ; *t.b.*, transverse band. Supporting substance shown hatched and shell substance stippled.

The lophophore is early zygolophous at a shell length of 2·8 to 3·5 mm. A small fragile hood is present on the posterior end of the septum : crura are present (Fig. 6A).

At a shell length of some 4·0 mm. the lophophore is late zygolophous (Fig. 6B). The hood is wide, as in the specimen figured by Thomson (1915, fig. 4, reproduced 1927, fig. 88h) at a shell length of 6·0 mm. By resorption of the posterior region of the hood there is now a band over the septum ; the two growth zones of the lophophore overlie it. The descending branches are complete : Thomson (1915, 1927) has shown that the descending branches grow from both crura and septum in *Terebratella inconspicua*. A smaller specimen (3·6 mm. long), but of the same stage, was sectioned, and certain sections are figured (Fig. 7). The small (*b.c.s.*) and great (*b.c.g.*) brachial canals are now clearly distinguishable. The anterior extremities of the coelomic or

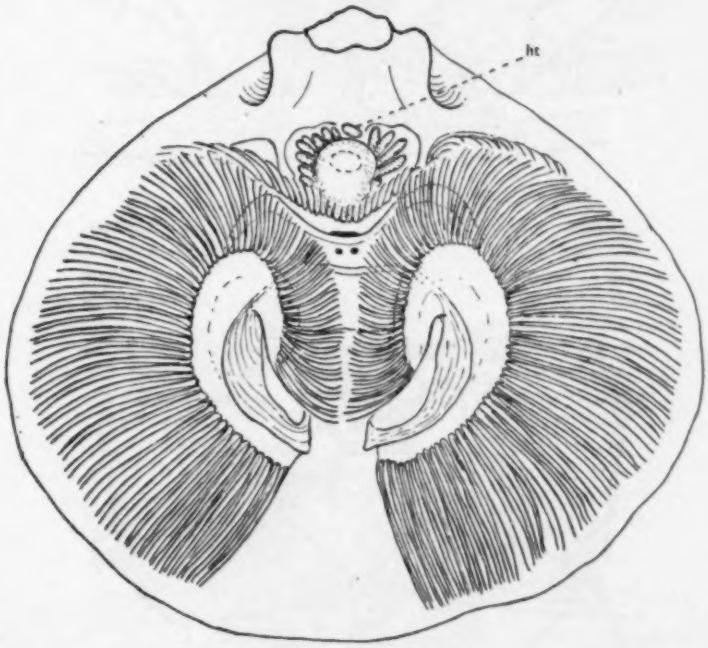
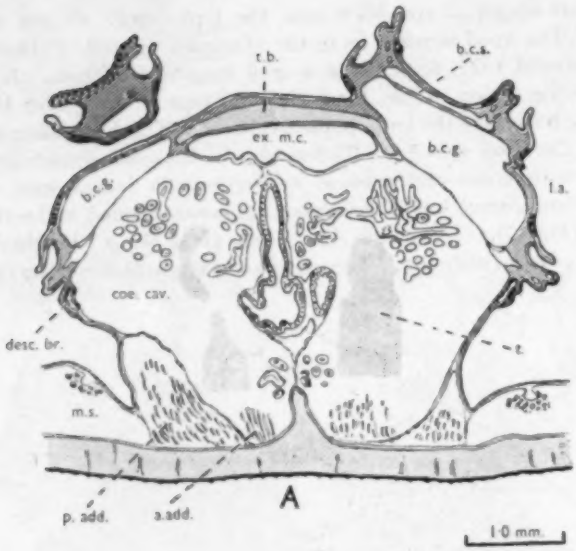


Fig. 8—*Terebratella inconspicua*. Brachial valve of a young adult of shell length 11·0 mm. and width 10·3 mm., with plectolophe. The ascending branches of the loop are broader than when fully adult. The intestine has been removed.
ht., heart.

visceral cavity may be considered the beginnings of the brachial pouches of Hancock (1885). At this size the posterior region of the lophophore is well above the valve floor, owing to the increase in thickness of the body (Fig. 7A). Figure 7B is through the growth regions of the lophophore and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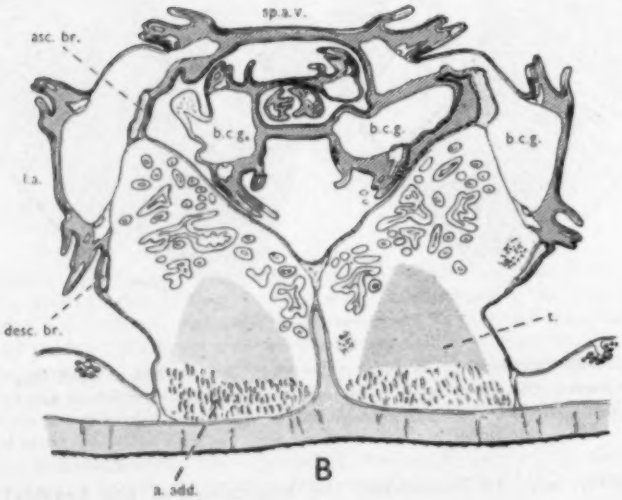
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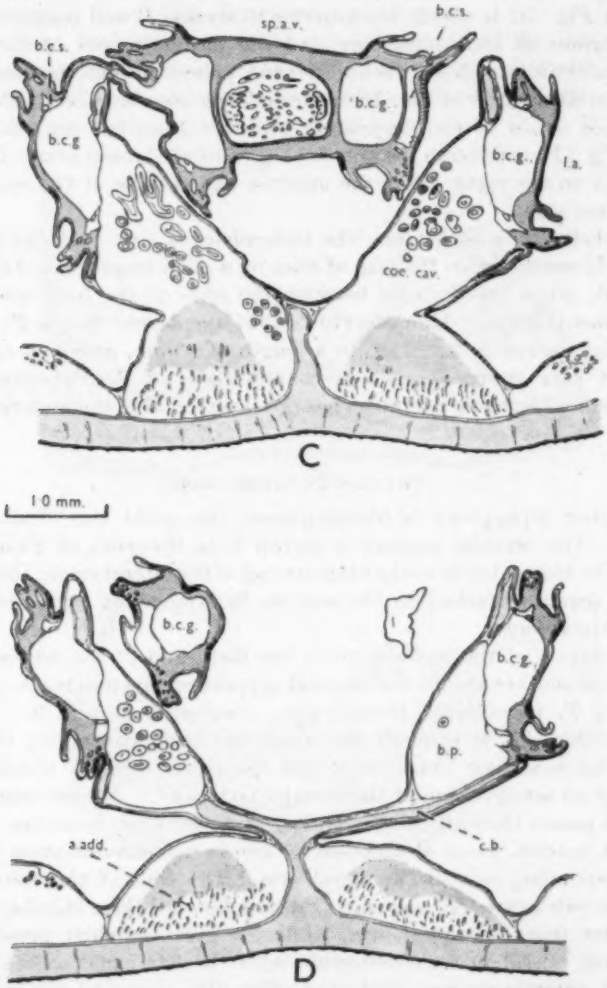

Fig. 9.—*Terebratella inconspicua* of shell length about 15 mm. Transverse sections of the brachial valve with plectolophe, (A.) in the region of the transverse band (*t.b.*); (B.) through the twin growth regions at the apex of the spiral arm; C. through region where lateral and spiral arms are becoming separate; (D.) through the bands connecting the descending branches of the loop with the septum.

c.b., connecting band., *ex.m.c.*, extension of mantle cavity; *p.add.*, posterior adductor muscle; *sp.a.v.*, ventral surface of spiral arm; *t.*, tendon of adductor muscle. Other lettering as in Fig. 7.

the transverse band of the loop : the small space dorsal of the band is an external space formed by the posterior invagination of the body wall. The section in Fig. 7C is about 48μ anterior to section B and passes through the growth regions of the lophophore and the posterior part of the ascending branches of the loop. A section anterior to C passes through the hood (Fig. 7D). The section illustrated in Fig. 7E is through the anterior part of the hood and the anterior origin of the descending branches from the septum. The last section (Fig. 7F) is through the anterior region of the lateral arms of the lophophore, and on the right shows the anterior recurvature of the small brachial canal of that side.

At a shell length of 5·2 mm. the lophophore is very early plectolophous ; the hood is nearly twice the size of that at a shell length of 4·0 mm., shown in Fig. 6B, while the distance between the edge of the hood and the bases of the filaments is less. Thomson (1915, 1927) mentioned that in *T. inconspicua* a hood may persist in shells up to a length of 6 mm., although apparently a small and very transient hood is characteristic of the development of *T. inconspicua*. The latter condition has not been found in the material examined by me.

THE ADULT LOPHOPHORE

The adult lophophore is plectolophous, the spiral arm short and broad (Fig. 8). The brachial support is known from the work of Thomson (1915, 1927). The loop extends to the extreme end of the lateral arms : the descending branches remain attached to the septum by connecting bands in the adult. Spicules are absent.

The relation of the lophophore to the body and of the lateral and spiral arms to one another and to the brachial support is shown in transverse sections through a *T. inconspicua* 15 mm. long, illustrated in Fig. 9. The section shown in Fig. 9A is through the transverse band connecting the posterior ends of the ascending branches of the loop, and beneath which is a space formed by an invagination of the anterior body wall. A more anterior section (Fig. 9B) passes through the descending and ascending branches of the loop. The great brachial canal of each lateral arm is in communication with that of the corresponding side of the spiral arm. The coils of the spiral arm, one within the other, are well shown. Further forward (Fig. 9C) the right lateral arm is free from the spiral arm, while the great brachial canal of the left lateral arm is still in communication with the left canal of the spiral arm. The most anterior section illustrated (Fig. 9D) passes on the right through the band connecting the descending branch with the septum. Both lateral arms are now free from the spiral arm, which is near its anterior limit. The visceral or coelomic cavity extends into the lateral arms as the brachial pouches, and at this level contain digestive diverticula, but further forward these are wanting.

Small brachial canals run at the bases of the filaments to which they give off branches ; within them run ' blood vessels ' (Fig. 10A). In each lateral arm a brachial pouch extends anteriorly to its extremity, reaching beyond the great and small brachial canals. The relation to one another of the small

and great brachial canals and the brachial pouch near the end of the lateral arm is shown in Fig. 10B. Williams's (1956) statement that a single brachial canal is present in *Terebratella* is evidently a misprint.

Muscle fibres, mainly transverse, occur in the walls of the small and great brachial canals, chiefly beneath the thick supporting substance underlying the filaments and food grooves. In sections this material is often seen compressed by contraction of the muscles.

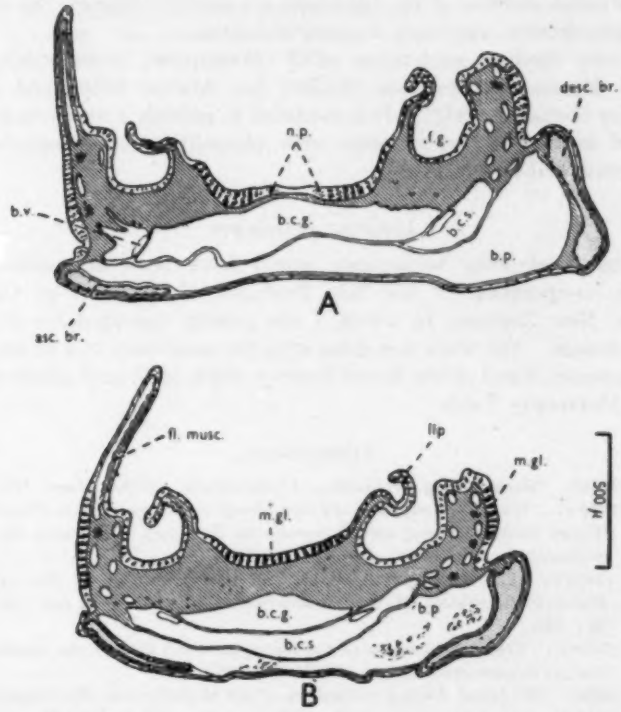

Fig. 10—*Terebratella inconspicua*. Transverse sections through lateral arm of a specimen about 15 mm. long, to show the relative positions of small and great brachial canals and the brachial pouch, (A.) near the middle of the length of the arm, (B.) near the tip, through the recurvature of the small brachial canal.
b.v., 'blood vessel'; *fl.musc.*, muscle in filament; *m.gl.*, mucous gland cells; *n.p.*, principal nerve. Other lettering as in Fig. 7.

The principal nerve (*n.p.*) only could be distinguished with certainty. The distribution of mucous cells on the lophophore is as follows: (1) a wide abfrontal tract below the bases of the filaments on both lateral and spiral arms; this tract is in the exhalant chamber: (2) a tract on each side of the brachial membrane and extending on to the outer surface of the lip of the food groove: (3) scattered mucous cells in the walls of the food groove. Mucous cells also occur on the filaments.

The filaments are in the usual double alternating series, the outer with grooved and the inner with ridged frontal surfaces. Behind the mouth some 16 or 18 filaments are in single series, and have ridged frontal surfaces. The filaments are supported by a cylinder of supporting substance within which runs the filamentar canal. Longitudinal muscles of the filaments have the usual arrangement, being most developed frontally and to a lesser degree abfrontally. The frontal group is of striated fibres.

The body of the lophophore is entirely ciliated, except possibly for mucous cells. The outer surfaces of the filaments are entirely ciliated, the cilia being in four tracts, frontal, abfrontal and paired lateral.

The ciliary feeding mechanism of *T. inconspicua* is essentially similar to that of *Macandrevia cranium* (Müller) (see Atkins, 1956), and is not as described by Richards (1952). It is intended to publish later a comprehensive account of feeding in brachiopods with plectolophous lophophores, when any variations will be considered.

ACKNOWLEDGMENTS

Work on *Terebratella inconspicua* would have been impossible without the active co-operation of the late Professor E. Percival of Canterbury University, New Zealand, to whom I am greatly indebted for sending me living specimens. The work was done with the assistance of a grant from the Browne Research Fund of the Royal Society, 1956–1957, and whilst occupying a London University Table.

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SURVIVAL VALUES OF DIFFERENT METHODS OF CAMOUFLAGE AS SHOWN IN A MODEL POPULATION

BY

EDWARD R. A. TURNER

*St. Luke's College, Exeter**

[Accepted 11th October, 1960]

(With 1 plate and 4 figures in the text)

Pastry "larvae" were coloured in different ways and offered in randomised samples on a lawn to wild birds. Small adaptive changes provided significant protection and included the following methods of camouflage :— background colour resemblance, disruptive coloration, countershading and disguise—a leaf mimic. General colour seemed of overriding importance in camouflage. Very tentative estimations were made of comparative vulnerability values for various methods of camouflage in relation to this particular experimental arrangement. A rather poor quality leaf mimic, a countershaded model and a disruptively coloured model had an approximately equal advantage over a well-matched plain standard green model, but the advantage was only equal to and certainly not more than a small colour change. Increased predation pressure enhanced the value of small adaptive advantages. Some evidence was found for the adaptive value of seasonal dimorphism. There was some indication that stable polymorphism might be based upon factors simpler than a balance of harmful and beneficial genes.

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INTRODUCTION

The general principles of camouflage (Cott 1957) have been studied for over sixty years and it is thought that animals conceal themselves by the following basic methods : (*a*) Coloration resembling that of the general background ; (*b*) Countershading, in which the colour on the dorsal surface is darker than the ventral surface. Uniformly coloured objects, when subjected to normal top lighting, are given the appearance of solidity due to the top appearing lighter than the bottom. This effect is counteracted by countershading (see Plate 1 A and B) ; (*c*) Disruptive coloration in which an animal employs fairly sharply contrasting colours that are present in the background. This arrangement breaks up the animal's outline and potential predators are thought to see several nondescript objects instead of the animal as a whole ; (*d*) Shadow elimination ; (*e*) Disguise in which the animal resembles some ubiquitous object of the habitat such as a leaf, etc. In this case the animal

* At present on research leave at Madingley Field Station, Department of Zoology, Cambridge.

does not disappear, but is perfectly visible ; but so are thousands of other very similar objects to which the predators have become habituated. The methods (*a*)–(*d*) depend less on habituation of the predator and more on the prevention of the predator's visual discrimination of the prey. It is highly significant that young animals will usually seize any object that contrasts with the background.

The main principles of camouflage theory appear to be reasonable but, so far, only a limited amount of work has been done to establish their validity, and little or none on their comparative values.

Popham (1941, 1943 & 1944) has demonstrated quite conclusively that Corixidae that match the general colour of their background have a better chance of survival than those that do not. With regard to countershading, de Ruiter (1955) compared the rate of predation by jays (*Garrulus glandarius*) of various lepidopteran larvae that were offered in normal and inverted positions, and found that the inverted larvae suffered the heaviest casualties. This experiment did not, unfortunately, compare the normal countershaded larvae with plain coloured ones. (An attempt was made by using plain painted larvae against the normal, but the numbers involved were too small to produce significant results.) It was argued, however, that the difference between the plain and the inverted was merely one of degree. Considerable indirect evidence was produced to add weight to the general argument. In addition de Ruiter (1952) has produced very good evidence of the effectiveness of the disguise of stick caterpillars.

The present experiments were designed with the following objectives in view.

(1) To confirm that background colour resemblance and countershading can provide protection, and to compare, particularly, plain and countershaded types.

(2) To find out if disruptive coloration provides protection.

(3) To attempt to establish a rough quantitative estimation of the value of various methods of camouflage.

(4) By chance, it was possible to investigate an aspect of disguise.

(5) An important principle of evolutionary theory is the selective value of small changes. It was hoped that the experiments might produce evidence in this connection.

METHOD

An investigation into the value of any supposed method of protection requires two sets of animals ; one with, and one without the presumed adaptive character that is being investigated. Even if two such sets are found, it can never be assumed that they are identical in every other respect, and therefore even if differential predation was shown to occur, it could not be unequivocally attributed to the supposed adaptation. In addition, the predator used may be familiar with one of the types, and is already positively or negatively habituated to it from a feeding point of view. Another problem is that the predator and prey must be presented in their normal habitats under natural conditions, and this may involve sampling techniques and their associated

hazards. To obtain satisfactory results, large numbers of the animals will be required, and lastly, with living animals the possibility of investigating the comparative aspects of camouflage is remote.

Most of these requirements could, however, be met by making edible model prey and offering them to a wild population of birds against a uniform background. Unlike animals, the models could be guaranteed to differ only as required for the experiment.

Models shaped like larvae (Plate 1 B) were made from raw pastry consisting of a mixture of three and a half parts flour to one and a half parts of lard. This mixture is of about the same consistency as plasticene and can be moulded into almost any shape. It is a good food, containing carbohydrate, fat, and vitamin B complex, and is very attractive to birds. It is very stable and can be easily coloured. British Drug Houses kindly supplied a selection of tasteless culinary dyes from which practically any colour could be produced. (The white models were normal uncoloured pastry.)

There is of course no guarantee that the birds could not taste the dyes but they were used in very dilute concentrations (one in several thousand) and only applied superficially. Subsequently the dyes have been used extensively and birds of several different species have accepted painted models with great enthusiasm. Crows in particular seem quite prepared to eat anything and during unsuccessful attempts to find a coating that would render the models unpalatable for the purpose of investigating aposematic coloration, they ate with apparent relish pastry flavoured with concentrated aloin solution, colocynth powder, tincture of capsicum, and large quantities of tartar emetic! (The author would in fact be very pleased to learn of any coating that crows might find distasteful to the point of instant rejection.) In addition the crows were invariably in a hurry because of my appearing when they had consumed the required amount, which normally took only a few seconds. From their behaviour I am quite confident that when they spotted a model it was eaten instantly, without any colour preferences being indulged.

Models showing different methods of camouflage (see Plate 1) were offered on a large lawn to the birds frequenting the author's garden in Devon. In experiments 1 and 2 a variety of birds were involved, but in the remainder the predators were exclusively a pair of wild crows (*Corvus corone*) that, after training, very obligingly obeyed a summons at the author's whistle or blast on a hunting horn. The other birds were discouraged by the crows and kept away from the experimental area.

The basic plan in each experiment was to offer simultaneously equal numbers of two or three types of standardized models in a randomized manner (see Fig. 1). When, as near as could be judged, one half of the models had been consumed, the birds were driven off and the remaining models counted. Trials were continued daily until significant results were obtained. This was a reasonable procedure because the overall results were extremely consistent in all cases, and an example of this can be clearly seen in the smoothness of the curves shown in the graph (Fig. 4) which show the numbers of different models consumed during experiment 4. The birds were very wild and it was

not possible to obtain consistent readings for the times taken. The crows were incredibly proficient at finding highly cryptic models and would find in a matter of seconds models most difficult for humans to detect.

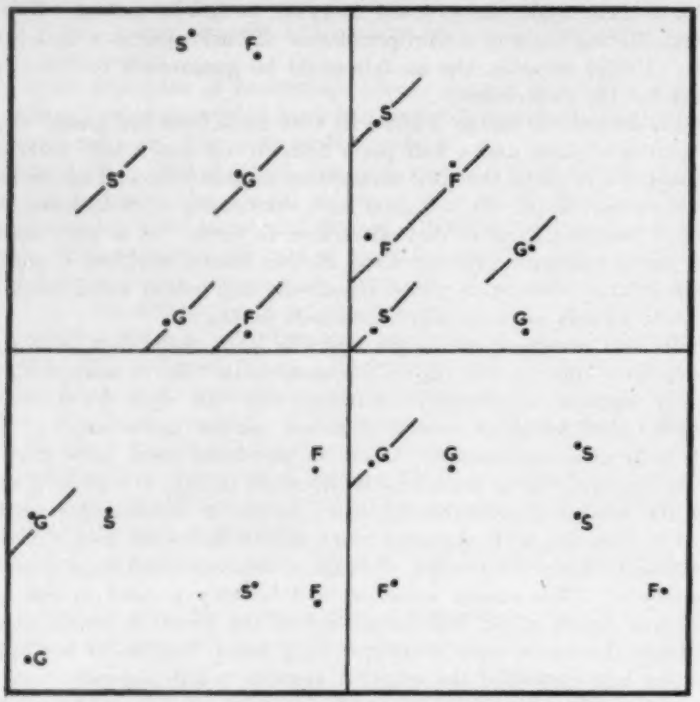

Fig. 1.—Distribution chart. Total eaten. Fawn (F) 3 11th Nov. Dull
Green (G) 5
Stripe (S) 3 7.30 a.m.

The above is a copy of one of the charts used, and shows how the experimental area was divided up into 4 × 25 square yards with a stake in the middle of each. A hundred cards were made and divided into 4 packs each containing 2 fawn, 2 green and 2 striped, and also 19 blanks. The cards indicated the position of the model in relation to the stake, e.g. F. means fawn model at 3 o'clock from the stake. The cards were shuffled and dealt for each trial, and the quarters were revolved.

Experiment I.—Background colour

Each day equal numbers of white and standard green (Rinneman's Green, Ridgeway 1912) models were offered. (Standard green was a good overall match for the colour of the lawn.)

Predators. Great tit (*Parus major*), coal tit (*Parus ater*) and chaffinch (*Fringilla coelebs*).

Results. See Table 1.

Comments. Many more whites were consumed than standards (P 0·01) and thus the green coloration provides a high degree of protection. During the first four trials the birds became more confident, and in the last trial the

models were eaten much more quickly. From Table 1 it can be seen that the ratio of the numbers of white models eaten and not eaten, changed from 63 : 44 to 24 : 4 and the green ratio changed from 40 : 67 to 6 : 22. It therefore seems that with increasing predator pressure the advantage becomes increasingly in favour of the better adapted model and relatively fewer are eaten. Both sets of figures are significantly different. (P=0·01.)

Table 1—Comparison of the numbers of models eaten and not eaten in the experiments.

	White		Standard Green		Light Green		Counter-shaded		Fawn		Disruptive		Proba-bility
	Eaten	Not eaten	Eaten	Not eaten	Eaten	Not eaten	Eaten	Not eaten	Eaten	Not eaten	Eaten	Not eaten	
Exp. 1 Total	87	48	46	89									0·01
Trials 1–4	63	44	40	67									0·01
Trial 5	24	4	6	22									0·01
Exp. 2 Total			78	122	106	94							0·01
Exp. 3 Total			107	58			79	86					0·01
Exp. 4 Total			145	87					147	85	116	116	d 0·01
Trials 1–5			21	19					33	7	18	22	a 0·01
„ 1–13			57	47					75	29	50	54	a 0·01
„ 13–26			72	32					59	45	56	48	b 0·05
(„ 26–29)			16	8					13	11	10	14	
													c 0·05
													e 0·05

a. Significance between figures for Fawn and those for Green and/or Disruptive.
b. Significance between figures for Standard and those for Fawn and/or Disruptive.
c. Significance between figures for Standard for first 13 days and for second 13 days.
d. Significance between figures for Disruptive and for Fawn and/or Standard.
e. Significance between figures for Fawn for first 13 days (non-mimic) and for second 13 days (mimic).

Experiment 2.—Small colour change

Models exhibiting two different tones of the same green were offered. The differences were not great and the colours can be described as midgreen (Standard) and a fairly pale green (Deep Turtle, Ridgeway 1912). The pale green was prepared by diluting the standard green.

Predators. As for experiment 1.

Results. See Table 1.

Comments. A slight colour change can give a significant degree of protection.

Experiment 3.—Countershading

Equal numbers of standard green and countershaded models were offered. The preparation of the latter models was difficult and considerable time was expended making them. Experiments were conducted with the author's children to ascertain the best method of colouring the models and the countershading of the final choice was considered to be effective (see Plate I). The

same colour (Standard Green) was employed in both types of model but the upper dorsal surface of the countershaded type received an extra coat of dye and the lower ventral surface was left almost white.

Predators. Crows.

Results. See Table 1

Comments. Countershading of the type used in this experiment provides significant protection.

Experiment 4.—*Disruptive coloration*

This experiment was more involved. Disruptive coloration consists of at least two colours and therefore two models must be used as controls to ensure that if there is a selective effect in favour of the disruptive type, then it must be demonstrated that it is not due to the addition of a second colour of higher cryptic value.

The summer of 1959 was a dry one in England and the lawn contained a fair amount of dead grass. A model was designed with a background of standard green, and a fawn dorsal stripe was added (see Plate 1). The two control models were standard green and plain fawn respectively. The fawn was a good match for the Isabella Colour of Ridgeway (1912).

Predators. Crows.

Results. See Table 1 and Fig. 4.

Comments. Models employing two contrasting colours from the background are given a significantly higher protection than models that are plain coloured with either colour.

DISCUSSION

Before comparing the results of the experiments, possible sources of experimental error that may tend to produce false conclusions must be first considered.

During the individual daily trials of each experiment, the proportion of the different models would change. For example, if one of the models was at an advantage the predator would take more of the other type at the beginning of the experimental trial, and thus the density of the inferior model would drop. The predator would therefore encounter relatively more of the superior type, and their risk would be higher than it was originally. Figure 2 shows this very clearly. The effect would be to produce a minimal value for the adaptive character, particularly if the advantage was great. In recognition of this difficulty the experiments were concluded when one half of the models were consumed, so that conditions were more or less constant in this respect.

The habitat changed slightly during each group of trials. The lawn was a large one and it was quite out of the question to cut it daily because of the labour of removing and replacing the 100 marker stakes (see Fig. 1). The rate at which the grass grew varied with the weather and the standardized mowing was of no certain value in keeping conditions constant. The experiments were, however, spread out over a considerable period, and so there were probably no great inter-experimental differences in this respect. The colour of the lawn also seemed to vary slightly with the weather. The predators became more confident as time went on, but the improvement in their detection reached its maximum fairly quickly.

These sources of error cancel themselves out to a certain extent and it is not considered that they constitute a serious objection to the use of the figures from a comparative point of view.

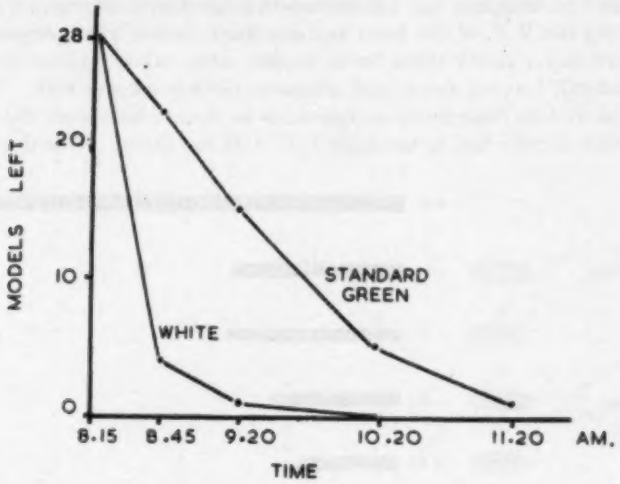

Fig. 2.—Graph showing changes in the proportions of two types of models during an experiment.

Specific experimental differences

In experiment 1 the randomization was not considered to be quite perfect because the position of the models to the stake was not randomized, but the models were placed haphazardly. The result of experiment 1 was so obvious that it could not have been affected by a very small error in this respect. Apart from this minor point, experiments 1 and 2 are reasonably comparable. Experiments 3 and 4 were also carried out under basically similar conditions but they differ from 1 and 2 in being at lower densities, and in that the predators were crows.

It seems reasonable, therefore, to make a comparison between the results of experiments 1 and 2, and also between 3 and 4. Discretion must be exercised in comparing the results of the two groups.

In all the experiments a standard green model was employed as a control. The effectiveness of the other models' camouflage can therefore be compared by relating their consumption to that of the standard model. If we consider the standard model to have a Vulnerability Value of I the comparative protective values of the other models can be expressed as :

$$\text{*Vulnerability Value (V.V.)} = \frac{\text{Numbers of models consumed}}{\text{Numbers of standard greens consumed}}$$

Standard Green V.V. $= I$.

The results are shown in Fig. 3.

* For a statistical treatment of the significance of the comparative V.V. see Appendix. If V.V. are compared in the text it can be assumed that they are significantly different at the 5 per cent level.

One aspect of camouflage appears to be dominant to all others and that is the general importance of colour resemblance. The white models show a high vulnerability value of 1·9, and if the significant figures of trial 5 (Exp. 1) are used the V.V. becomes 4. The dominant importance of colour is confirmed by comparing the V.V. of the fawn and standard models in experiment 4. In the first five days, thirty-three fawn models were taken against twenty-one of the standard, leaving seven and nineteen models respectively. The fawn models were at this time fairly conspicuous in comparison with the standard ones, and this is reflected in the high V.V. 1·32 for fawn. This figure can be

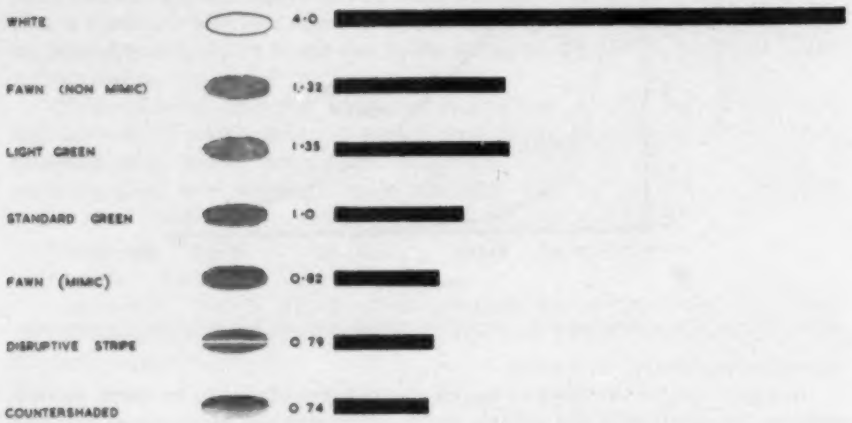

Fig. 3.—Vulnerability Values. Comparative protective values of the methods of camouflage used in the experiments.

compared with the values of 0·74 and 0·79 for the countershaded and disruptive models respectively. In experiment 2 the V.V. for the light green models is 1·3 and this is at a higher density than for the experiments testing the other types. It can probably be assumed that the V.V. for light green is rather low, but even taking it at its face value, it shows that the countershaded and disruptive models have an additional protection equivalent to not more than a small colour advantage.

With reference to experiment 4, an examination of Fig. 4 and Table 1 will show that after the first five trials, the predation rate of the fawn models fell slowly, and in the second thirteen trials of the experiment the number taken was below that of the standard model. For the first thirteen trials the V.V. for fawn was 1·6, but for the second thirteen days it fell to 0·82. Table 1 and the Appendix show that there is a significant difference in the ratios of fawn models eaten and not eaten during these two periods. The reason for this curious result was the presence of a row of willow trees (*Salix* garden sp.) bordering the experimental area. It was noted on the third day of the experiment that a few leaves were beginning to fall and that they were a fair match for the size of the models, and one or two matched the colour

of the fawn models. In due course the lawn was covered with a large number of these leaves and as time went on their colour changed to a fawn that was an excellent match for the model. The effect is most clearly reflected in the graph which shows a gradual decrease in the numbers of fawn models eaten in relation to the other models.

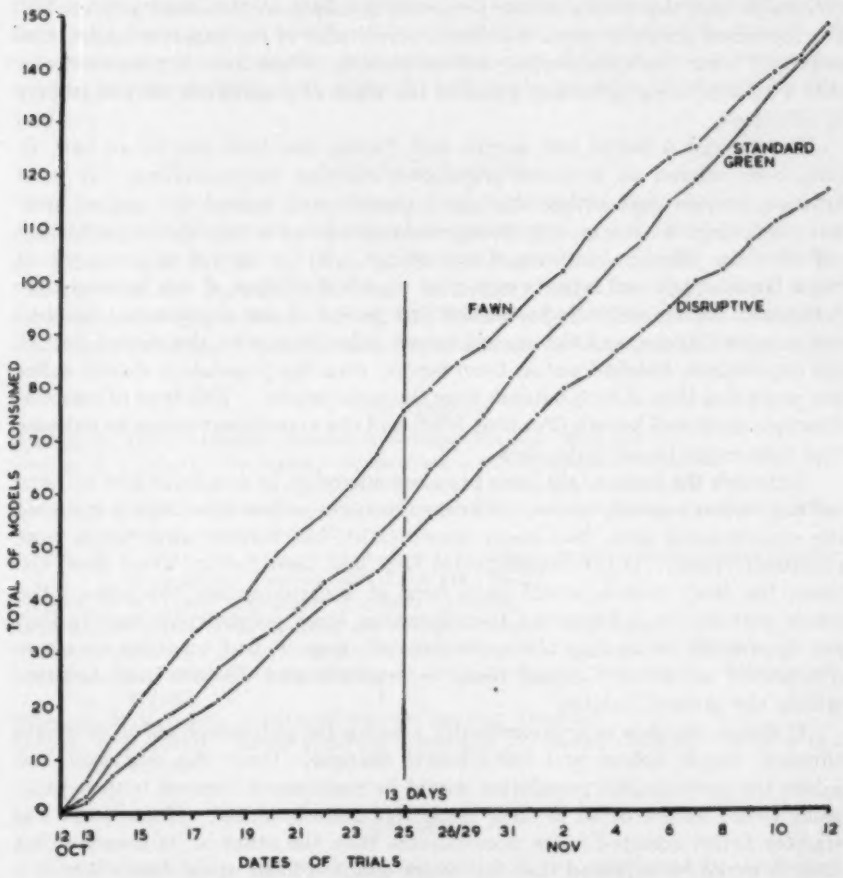

Fig. 4.—Graph showing results of experiment 4 (see text).

The fawn models, through the effect of the fallen leaves, had changed from fairly conspicuous fawn objects to moderately successful leaf mimics ; they were still easily seen, but so were hundreds of other objects of similar appearance. Owing to a slight change of circumstances in the habitat the models had been changed from indifferent " self effacers " (Cott 1957) to quite

successful "impostors". Self effacing animals are contemporary artists that represent the environment in abstract; the impostors are traditionalists producing a true copy of an object from the habitat.

In the first half of the experiment, the number of standard models taken was only slightly greater than that of the disrupted type. Later the position changed, and, as the fawn intake dropped, the difference between the standard and disruptive model intake became exaggerated. The fawn model was less vulnerable and this increased the predation pressure on the other two models The increased pressure improved the survival value of the superior model, and relatively fewer disruptive types were consumed. Thus there is more evidence that with increasing predatory pressure the value of a small adaptive character is enhanced.

Experiment 4 lasted one month and during this time the crows had, in fact, been offered an artificial population showing polymorphism. It is of interest to note that within this short period—and indeed the critical time was much shorter—a complete change had taken place in the relative protective values of the different methods of camouflage. In the case of an insect which has a larval stage and lays its eggs over a period of time, it can be seen that if the first brood, coinciding with the first period of the experiment, hatched out as green larvae, and the second brood, coinciding with the second half of the experiment, hatched out as fawn larvae, then the population should suffer less predation than if both batches were the same colour. This type of seasonal dimorphism is well known (Poulton 1890) and the experiment seems to indicate that this could be advantageous.

Although the lawn might have been considered to be a more or less uniform habitat, it was patently not so. The area near the willow trees, which included the experimental area, had many leaves on it, but further away there were practically none. If the experimental area had been further away from the trees, the fawn models would have been at a disadvantage throughout the whole period. It is suggested therefore that some polymorphic species that are apparently occupying the same habitat, may in fact have its members distributed at certain critical times in separate and distinct microhabitats within the general habitat.

If this is the case it is theoretically possible for polymorphism to originate through simple colour and behavioural changes. Once the mutation had arisen the polymorphic population would be maintained because both populations would be protected in their respective microhabitats. If one form was slightly better adapted in its microhabitat than the other in its microhabitat then it would be expected that the better adapted form would be present in a higher concentration than the other; the slight disadvantage of adaptation would thus be compensated by its lesser numbers, and predators might tend to find and eat the more common type (see Sheppard 1958, chap. 5).

Another way in which stable polymorphism could occur is by the result of a single colour change. In experiment 4 the samples showed a clear change in selection from fawn to green during the course of the trials. But the overall totals of models eaten was 147 fawn to 145 green. If all fawn or all green models had been offered over the experimental period it seems possible that

the predator would have become more proficient with only one type to contend with, and the population might thereby suffer increased predation.

It seems that a polymorphic population could originate from a single colour mutation. Subsequently no doubt the two forms would be subject to disruptive selection (Thoday 1959) and considerable differences in the gene complex would be expected, and a stable polymorphism would result.

The experimental results indicate that if an animal's life span is such that it occupies a habitat that is subject to frequent change, then its camouflage may have to be a compromise. This may account for the paucity of extreme examples of camouflage in countries such as Great Britain where the seasons are so variable and unstable and cause continuous change in the habitat.

ACKNOWLEDGMENTS

The author is particularly grateful to the following for their encouragement, and most helpful advice in the preparation of this paper. Professor Dr. L. de Ruiter, and Drs H. B. Cott, C. B. Goodhart, R. A. Hinde, and W. H. Thorpe, F.R.S. In addition, some extremely valuable suggestions have been made by the editors. Mr A. M. Walker of the Cambridge University Statistical Laboratory gave invaluable assistance in the statistical treatment.

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APPENDIX

The Vulnerability Values (V) as calculated in this paper can be compared by calculating the standard error s_y of $y \log_e V$.

$$s_y = \log_e V \sqrt{\left\{\frac{1}{n}\left(\frac{1}{p_1} + \frac{1}{p_2} - 2\right)\right\}}$$

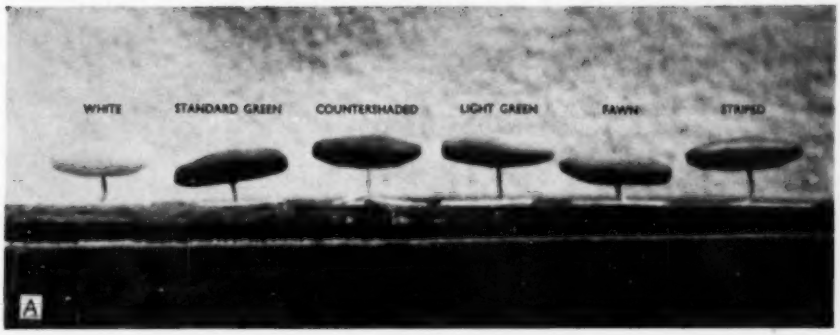
n=total number of models exposed. p_1=number of test models eaten. p_2=number of standard green models eaten.

The confidence limits for the true index can be calculated from the antilogs of $y - 1{\cdot}96\, s_y$ and $y + 1{\cdot}96\, s_y$.

If the intervals between the confidence limits derived from two different vulnerability values do not overlap, then the two values differ significantly at the 5 per cent level.

	n	p_1	p_2	V	$y \log_e V$	s_y	anti-log $y-1{\cdot}96s_y$	anti-log $y+1{\cdot}96s_y$
White	28	24	6	4·00	1·386	0·370	1·94	8·26
Light green ..	200	106	78	1·35	0·307	0·111	1·09	1·69
Counter-shaded ..	165	79	107	0·74	−0·304	0·099	0·61	0·90
Disruptive ..	232	116	145	0·80	−0·223	0·083	0·68	0·94
Fawn (mimic) ..	104	59	72	0·82	−0·200	0·108	0·66	1·01
Fawn (non-mimic)	104	75	57	1·32	0·275	0·108	1·07	1·63

It can thus be seen that there are significant differences at the 5 per cent level between White and Light Green OR fawn, and also between any of these three and Countershaded, OR Disruptive OR Fawn Mimic.



A. The various models used (Length 2¼ cm.).

B. Four models shown against the lawn background.
Countershaded. Standard green.
White. Light green.

A NEW GENUS AND SPECIES OF TREMATODE PARASITIC IN *MACRURUS FABRICII* (SUNDEVAL), A DEEP-SEA FISH

BY

Z. KABATA

Marine Laboratory, Aberdeen

[Accepted 11th October 1960]

(With 5 figures in the text)

Twenty specimens of a trematode, hitherto undescribed, were found in *Macurus fabricii* caught off the coast of Iceland. They are described, figured and named in this paper.

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INTRODUCTION

A female specimen of *Macrurus fabricii* (Sundeval), a relatively rare fish inhabiting the continental slopes, was landed in Aberdeen by S/T *David Ogilvie* on 29th August 1958. The fish, 74·5 cm. long, was taken by trawl at the depth of 340 m., 45 miles ESE of East Horn, Iceland. The fish was sent to the Marine Laboratory, Aberdeen, where it was examined for parasites.

No parasites were found in the muscles or internal organs other than the intestinal tract which was infested by eighteen acanthocephalid worms identified as *Echinorhynchus gadi* Zoega. It also contained twenty specimens of a digenetic trematode which seems to belong to a new species.

In spite of the fact that the fish had been dead and stored in ice for some 7 to 14 days, the worms were still alive, though in a state of contraction. They were relaxed by placing them in a Petri dish containing fresh water for 30 minutes, after which some of them were prepared in a standard manner between slides, while others were stored in 4 per cent formalin. The description is based on the examination of such flattened and unflattened specimens and also transverse and sagittal serial sections, 9 μ thick, stained in Ehrlich's haematoxylin.

Specimens of the newly described trematode are deposited in the British Museum (Natural History), London. Reg. No. of the holotype specimen : 1960. 11. 14. 1. Reg. No. of five paratype specimens : 1960. 11. 14.2–6.

BATHYCREADIUM FLEXICOLLIS, gen. et sp. n.

Body small to medium size (Table 1), fusiform, with some degree of dorso-ventral depression, which is more pronounced in the posterior region ; more

or less uniform in width. Oral sucker slightly subterminal, opening obliquely downwards (Fig. 1a). Ventral sucker close to the anterior tip of the body, at a distance from it about equal to the width of the body (Table 1) and situated at the summit of a conspicuous, transversely oval swelling (Fig. 1a, c). Both suckers subglobular, provided with slit-like transverse openings with smooth margins, the ventral sucker being about twice the size of the

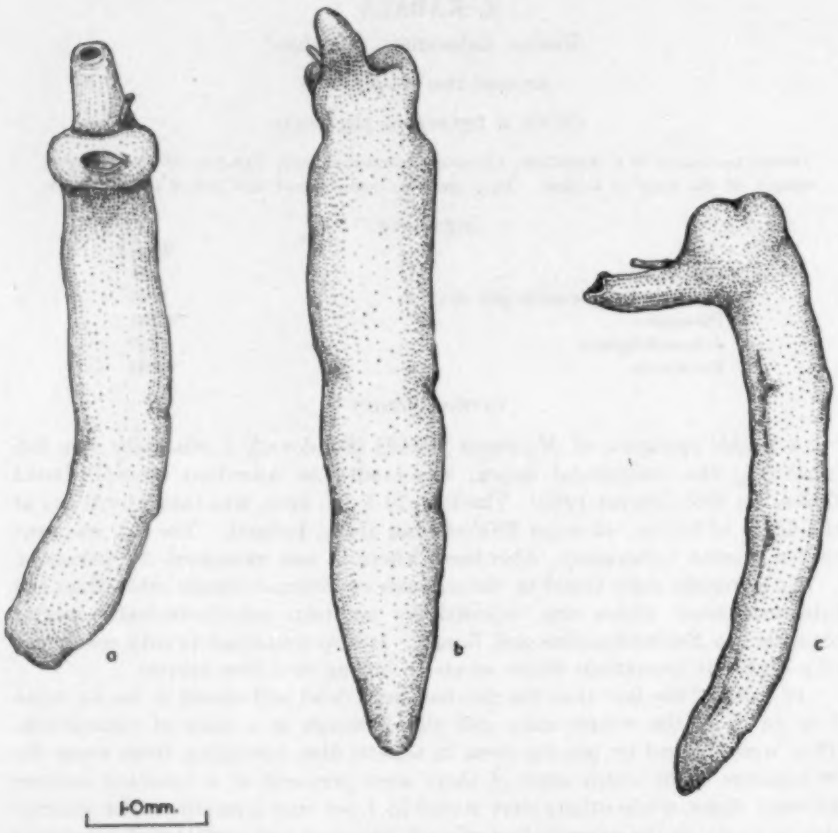

Fig. 1—*Bathycreadium flexicollis*, general view of three specimens: (a) ventral view, (b) dorsal view, (c) lateral view.

oral. The region between the suckers is narrower than the rest of the body and forms a tapering "neck", usually observed in dorsiflexion (Fig. 1c), which suggested the specific name of the worm. In the post-testicular region the body tapers slightly, ending in a more or less bluntly rounded tip. The cuticle is smooth. The colour of the living specimens is white, vitellaria appearing dark grey and reproductive organs brown through the translucent

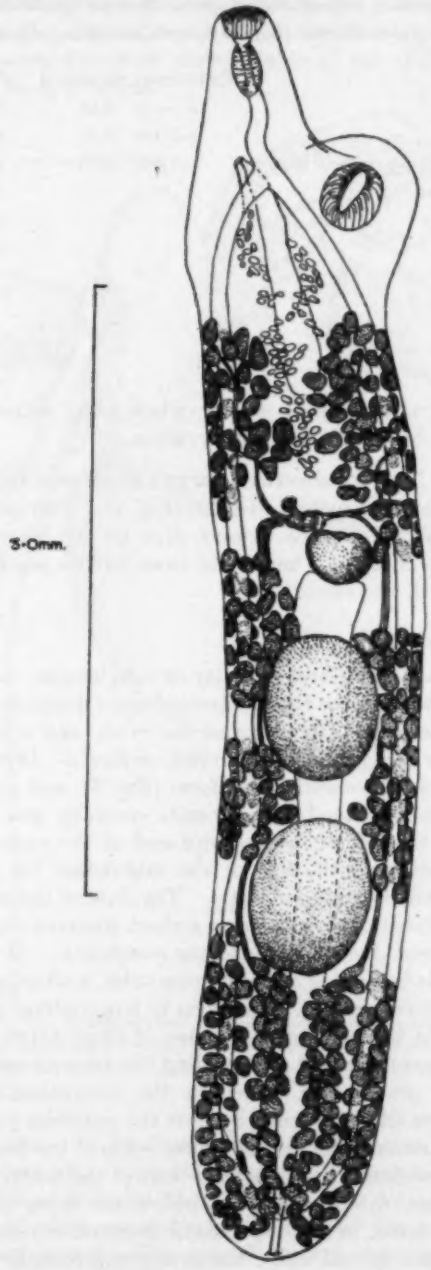

Fig. 2—*Bathycreadium flexicollis*, flattened specimen showing arrangement of internal organs.

Table 1—Dimensions of flattened and unflattened specimens of *Bathycreadium flexicollis*. Ranges are given, with means in parentheses. (Eggs in microns, remaining measurements in mm.)

	Unflattened specimens	Flattened specimens
Total length	4·2–6·2 (5·0)	6·6–11·0 (8·5)
Width	0·6–1·0 (0·7)	0·9 – 1·4 (1·2)
Distance from the anterior tip to ventral sucker	0·6–1·0 (0·7)	0·9 – 1·5 (1·2)
Diameter of the oral sucker		0·25 – 0·34 (0·30)
Diameter of ventral sucker		0·52 – 0·65 (0·59)
Dimensions of the ovary		0·39–0·43 × 0·39–0·43 (0·42 × 0·42)
Dimensions of testes		0·69–0·87 × 0·64–0·86 (0·82 × 0·75)
Dimensions of eggs		19·0–25·0 × 12·5–15·0 (22·0 × 14·5)

body wall. Uterine area appears yellow, when filled with eggs. Colour is not greatly affected by death and preservation.

Alimentary canal : A very short prepharynx is followed by a well developed pharynx and oesophagus of medium length (Fig. 2). The gut bifurcates near the ventral sucker and the caeca extend close to the lateral walls without enlarging along their course. They unite close to the posterior end and do not communicate with the exterior.

Reproductive system :

(1) *Female :* Ovary small and globular or subglobular, median or slightly submedian and displaced to the right. Immediately dorsal to it is the vitelline receptacle, about one-third of the size of the ovary and receiving two ducts from each side, there being no common vitelline ducts. Dorsal to that organ is the seminal receptacle, somewhat reniform (Fig. 3), and at the left anterior corner giving off Laurer's canal. This bends ventrally and extends postero-dorsally, passing to the left of the anterior end of the excretory vesicle and opening to the exterior on the left of the mid-dorsal line, about half-way between the ovary and the anterior testis. The duct of the seminal receptacle is joined by a convoluted oviduct to form a short common duct, which in turn is joined by the efferent duct of the vitelline receptacle. At the point of that junction, marking the beginning of the uterine tube, is situated a large Mehlis's gland (omitted for clarity in Fig. 3 but seen in longitudinal section in Fig. 4). This organ surrounds the area of confluence of these three ducts, extending between the female genitalia and surrounding the anterior part of the vitelline receptacle. Uterus pre-ovarian, coiled in the intercaecal field, metraterm absent. Genital pore situated ventrally near the posterior part of oesophagus. Vitellaria follicular, situated along the lateral walls of the body and extending from the haptorid swelling to the posterior end of the body. They are found both in the lateral and intercaecal fields, sometimes being grouped round the caeca. They are divided, in some specimens more clearly than in others, into four groups along each lateral wall : the first group extends back to the level of the ovary, the second between the ovary and the anterior testis, the third

is intertesticular and the fourth lies between the posterior testis and the end of the body (Fig. 2). The right and the left fourth groups are united by a duct. The eggs have a regular ovoid shape (Table 1), are of fairly uniform size and appear to have no operculum.

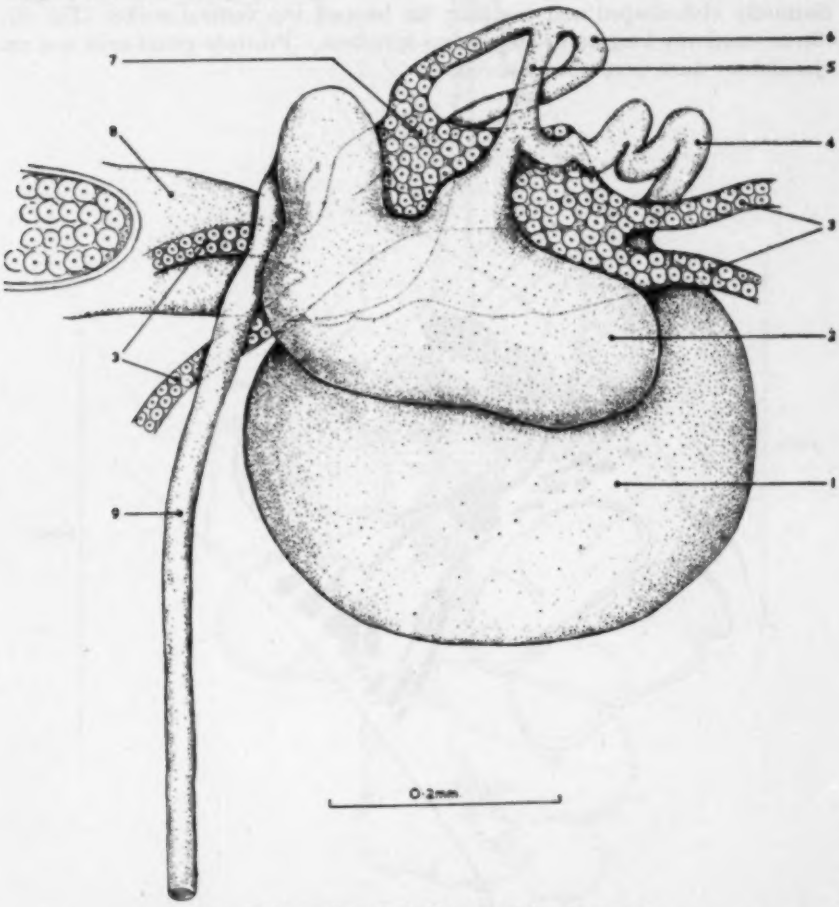

Fig. 3.—*Bathycreadium flexicollis*, central female organs :
1—ovary, 2—seminal receptacle, 3—vitelline ducts, 4—oviduct, 5—common duct of 2 and 4, 6—beginning of the uterine tube, 7—vitelline receptacle, 8—uterus, 9—Laurer's canal (Mehlis's gland omitted for clarity).

(2) *Male :* Testes two, in tandem and postovarian, situated about the middle point of the body. As a rule they are of the same size but they differ in shape from almost globular to ovoid (Fig. 2). Vasa efferentia leave the anterior testis at the left antero-lateral aspect and the posterior testis at the right antero-lateral aspect. The two ducts run close together in the post-ovarian region, passing ventrally to the anterior end of the excretory vesicle

and the ovary, but they diverge in the uterine region. They enter the posterior end of the seminal vesicle, apparently without uniting to form a common duct. There is no external seminal vesicle. The internal seminal vesicle shows several convolutions at the posterior end. Cirrus pouch well developed, distinctly club-shaped and reaching far beyond the ventral sucker (Fig. 5). Cirrus relatively long and slender, and spineless. Prostate gland cells and an ejaculatory duct were not observed.

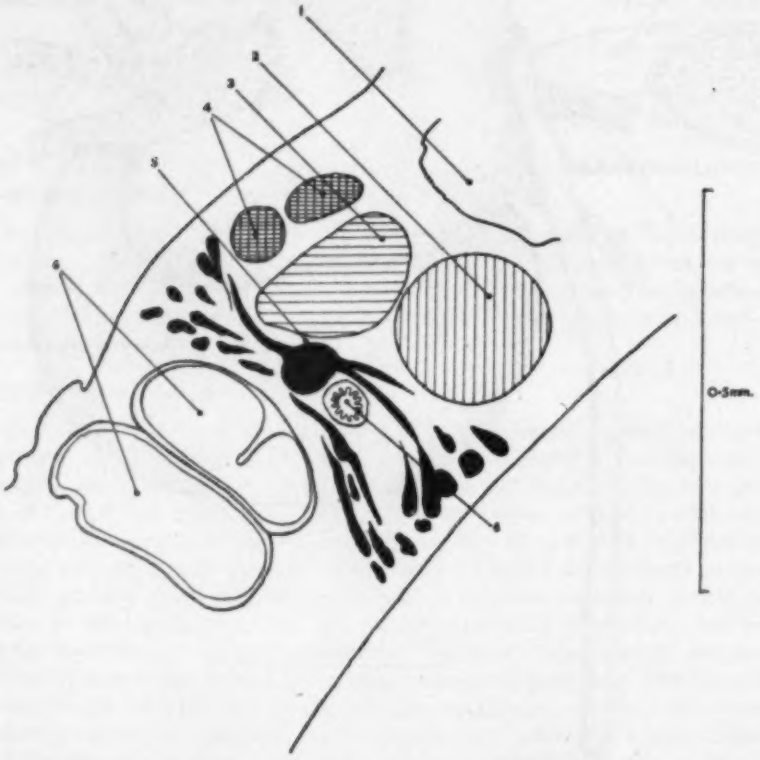

Fig. 4.—*Bathycreadium flexicollis*, longitudinal (sagittal) section through the region of female reproductive organs.
1—anterior end of excretory vesicle, 2—ovary, 3—vitelline receptacle, 4—seminal receptacle, 5—Mehlis's gland, 6—uterus.

Excretory pore terminal and having the shape of a narrow vertical oval. Excretory vesicle extending forward dorsal to the caeca and the posterior vitelline follicles to the level of the ovary. Dorsal to the testes it becomes flattened, enlarging in the intertesticular region so as to fill almost all available space.

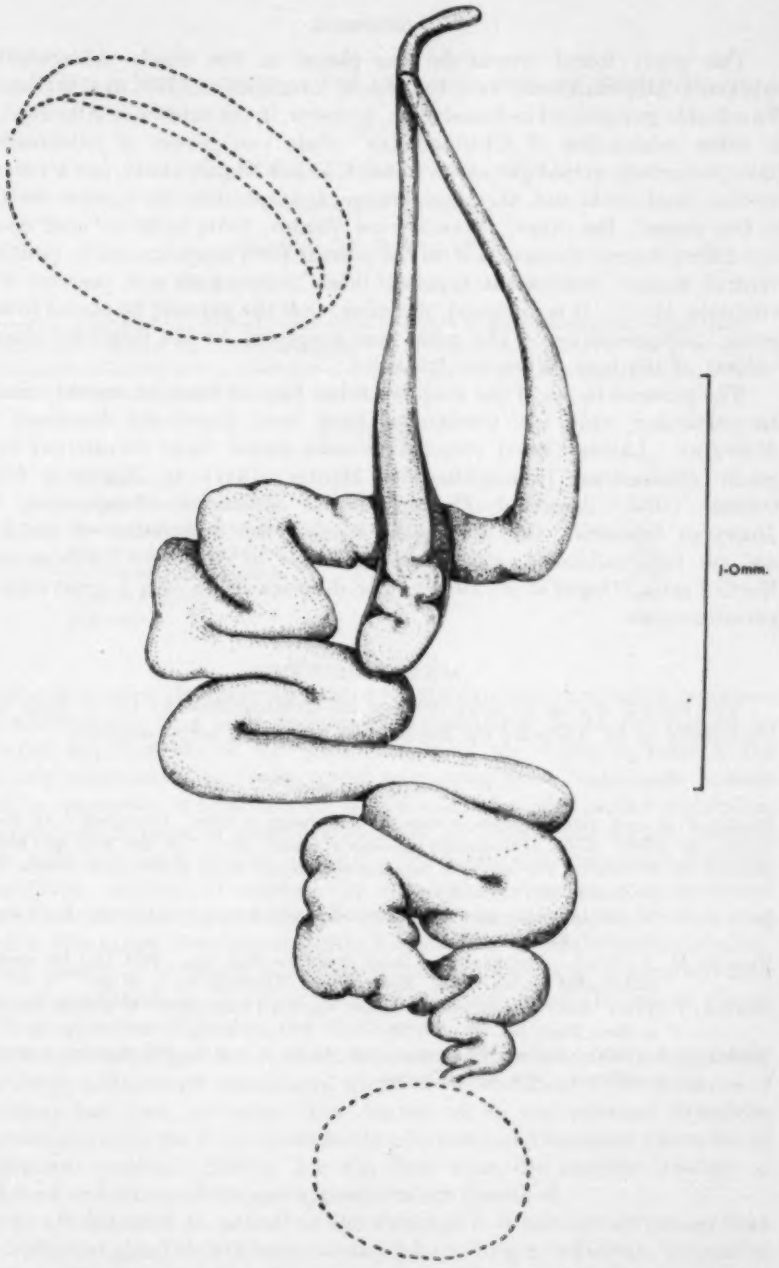

Fig. 5.—General position and shape of cirrus sac (cirrus everted). Positions of ventral sucker and ovary indicated in dotted lines.

DISCUSSION

The newly found trematode was placed in the family Allocreadiidae, subfamily Allocreadiinae, with the use of Yamaguti's (1959) key to Digenea. No suitable genus could be found for it, however, in the subfamily Allocreadiinae or other subfamilies of Allocreadiidae. Only two genera of Allocreadiinae have posteriorly united gut caeca : one, *Koseiria* Nagaty, 1942, has a ventrally opening anal canal and, therefore, cannot accommodate the species described in this paper ; the other, *Proenenterum* Manter, 1954, lacks an anal opening but differs in several respects from the present form (spinous cuticle, position of ventral sucker, lack of the typical " neck ", structure and position of the vitellaria, etc.).* It is proposed, therefore, that the parasite be placed in a new genus, *Bathycreadium*. The name was suggested by the relatively deep-sea habitat of the host, *Macrurus fabricii*.

The parasite fauna of the deep-sea fishes has not been extensively studied. In particular, only few trematodes have been previously described from *Macrurus*. Linton (1898) found *Distomum laevis*—later transferred to the genus *Dissosaccus* (Hemintidae) by Manter (1947)—in *Macrurus bairdii*. Odhner (1911) described *Proctophantastes abyssorum* (Zoogonidae) from *Macrurus rupestris*. One trematode species, the description of which has not yet been published, was found by Gusev in *Macrurus acrolepis* in the North Pacific (Dogiel *et al.*, 1958). The deep-sea fishes offer a great scope for parasitologists.

ACKNOWLEDGMENT

The author wishes to acknowledge his indebtedness to Dr C. Muir of the University of St Andrews for his help in preparing serial sections.

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* The known species of these genera occur respectively in marine fishes of the Red Sea and New Zealand waters. (Ed.).

THE RETROLINGUAL GLAND OF THE ELEPHANT

BY

A. J. E. CAVE, M.D., D.Sc., F.Z.S.

University of London

[Accepted 11th October, 1960]

(With 1 plate and 3 figures in the text)

Attention is directed to a hitherto overlooked structure in the elephant—the organ herein described and named the 'retrolingual gland'. A description is given of the gross and microscopical features of this gland and of the associated smaller pharyngeal glands. The function of these glands is discussed.

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INTRODUCTION

The mammalian glandular apparatus for the production of saliva manifests itself anatomically in a wide variety of topographical forms determined by particular requirements of the initial stages of the digestive process and accurately summarised by Owen (1868) as ranging from 'the simple mucous follicle to aggregates of three or more complex follicles, with further multiplications and compactions of secretory surfaces, in groups and bodies, forming glands and ducts with definite names'. The larger salivary glands (parotid, submaxillary, sublingual) conform to a relatively constant topographical pattern, but the minor glands (labial, buccal, molar, lingual, zygomatic, etc.) exhibit a wide range of variation both in location and in structural complexity, differing greatly in different mammalian forms and tending always by their degree of specialisation to reflect more particularly than the major glands specific peculiarities of dietary and mastication.

To the acknowledged list of these specialised minor glands must be added the hitherto undescribed retrolingual gland of the elephant. The presence of this organ has been no more than hinted at in the relevant literature (Mojsisovics, 1879), yet it is a sufficiently obtrusive and constant character of the elephant tongue. Herein, for the first time, its specific identity is established and its structure and appearance are described.

In so oft-dissected an animal as the elephant it is perhaps surprising that the retrolingual gland should have remained for so long overlooked: it must be remembered however that, to date, fewer than a dozen elephant specimens of the linguo-pharyngeal region have been submitted to a particularly detailed

examination, that the gland is situated deeply in the root of the tongue and that the difficulties inseparable from the dissection of unwieldy and unpreserved material are often considerable. (Indeed, these difficulties themselves may account for the dubiety which has long attended the precise incidence of the major salivary glands in the elephant. The parotid alone is recorded by all observers: the submaxillary was unnoticed by Watson (1874) and by Miall & Greenwood (1878) but was recorded by Forbes (1879) and by Eales (1926): the sublingual, undoubtedly wanting in the elephant, was erroneously stated to be present by both Mayer (1847) and Forbes (1879), who apparently interpreted as glandular the single, vertically compressed pad of gelatinous connective tissue situate behind the symphysis menti. Yet quite recently Grassé (1955) could assert the presence in the elephant of all three major salivary glands). A further consideration is that Watson's (1874) classical and influential paper, with its unfortunate and confusing preoccupation with pharyngeal 'pouches', focused the attention of later investigators upon particulars of pharyngeal constitution to the exclusion of minor structures in the mouth cavity and oro-pharyngeal isthmus. The modern investigation of elephant anatomy, which began with Perrault (1666–9), Moulin (1682), Blair (1710) and Camper (1802), was naturally confined to observations upon the major skeletal and visceral parts and upon the gross anatomy only of the tongue: and the later observations of Cuvier & Laurillard (1849), Harrison (1850), Hunter (1861), Goodsir (1868) and Owen (1868) likewise omitted detailed reference to the glandular adnexa of the tongue.

Mayer (1847), however, gave a more satisfactory description of the elephant tongue, noting its papillae and crudely figuring (though not recognising) the faucial tonsil. Subsequently more informative accounts of the morphological details of the elephant mouth and pharynx were given by Watson (1874), Miall & Greenwood (1878), Forbes (1879) and Mojsisovics (1879). These, to be duly supplemented by Eales' (1926) detailed study of the foetal African elephant, established the canon of the anatomy of the elephant mouth parts. Meanwhile Boas & Paulli (1908) had dealt with the sectional anatomy only of the elephant head and Sonntag (1922) had reviewed the number and arrangement of the lingual papillae. At all times the authoritative textbooks (Flower & Lydekker (1891), Weber (1928), Grassé (1955)) merely incorporated established findings without providing any additional direct information.

The relevant literature shows that the submucosal glands of the elephant tongue and bucco-pharynx have been accorded a passing attention by some investigators but have been largely ignored by others, and that the true nature of these structures has invariably been inferred on observational grounds rather than established by any more exact examination.

Thus Watson (1874) failed to recognise any distinctive glandular mass at the radix linguae. Miall & Greenwood (1878), however, regarded as 'doubtless glandular' the pits, 'densely aggregated' towards the tongue root, which are so characteristic of the pharyngeal mucosa: they noted the presence of 'similar glandular crypts' in the (unrecognised) faucial tonsil and of 'other flattened glands' in the glosso-epiglottic region. In the African elephant Forbes (1879) noted the tongue papillae and the pharyngeal glands ('irregular

raised glandular patches') which could 'attain a considerable size in the midline': he was silent as to any retrolingual gland, a structure impossible of confusion with discrete, if rather large, pharyngeal glands. In the same year Mojsisovics, likewise in the African elephant, recognised the faucial tonsil and correctly interpreted the perforate mucosal elevations of the pharyngeal walls as 'the papillae of, probably, gland duct-mouths'. His passing reference to 'the tongue root with its wealth of conglobulated glands' implies at least a superficial acquaintance with the retrolingual gland, which was not however recognised as an entity, or further described. Eales (1926) classified the oral glands of the foetal African elephant and noted the dorsum linguae to be punctured by gland orifices: she made no reference to any retrolingual organ.

Contrariwise Sonntag (1922), Ghetie (1944) and others omitted all reference to intrinsic lingual and pharyngeal glands in the elephant.

No previous writer has made explicit reference to the presence of a retrolingual gland, though Miall & Greenwood (1878) and Forbes (1879) hint at its occurrence and Mojsisovics (1879) may possibly have been acquainted with it. No previous investigator appears to have examined histologically the elephant's bucco-pharyngeal glanduar structures or to have interpreted functionally their nature and distribution.

MATERIAL AND METHODS

The spirit-preserved tongue and throat parts of two immature Asian elephants from the Zoological Society of London's menagerie were examined both macro- and microscopically. The first specimen (R.232) came from a female animal about two years old, the second (R.228) from a nine-year-old male. Dissection was made of the tongue, pharyngeal parietes and glosso-epiglottic region in both specimens, and in the better preserved younger specimen histological examination was made of certain glandular structures. These included the discrete, perforate, mammilliform elevations studding the mucosa of the pharynx and present in the mucosa of the postero-lateral aspect of the tongue, as well as the entire thickness of the retrolingual gland. Tissue removed was paraffin wax blocked and serially sectioned at 10μ and 12μ and the sections stained by haematoxylin and eosin.

ANATOMICAL OBSERVATIONS

The elephant tongue, markedly convex both antero-posteriorly and transversely, narrows suddenly behind the attachment of the wide and powerful anterior faucial pillar into a strikingly short, narrow, convex root of somewhat spatulate conformation, which presents two evenly rounded posterolateral extremities. In the younger specimen examined the radix linguae measures some 3·5 cm. long and 4 cm. broad: in the older specimen, 7 cm. long and 4 cm. broad. Its free surface faces successively backwards and downwards and lies in the closest apposition with the thick, muscular velum palatini. No median glosso-epiglottic fold is present, the rim of the velum being received into the floor of the single post-lingual vallecula, which is characterised by prominent transverse mucosal plicae. On the dorsal aspect of the velum lies the intranarial epiglottis (Fig. 1).

The mucous glands herein termed pharyngeal are liberally disposed in the mucosa of the oro-pharyngeal region. They occur on the postero-lateral aspect of the main portion of the tongue itself, upon the broad anterior faucial pillars, in the tonsillar fossae and the isthmus faucium, in the vallecula and in the piriform recess. As Miall & Greenwood (1878) and Forbes (1879) noted, they tend to increase in number and size as the vallecular region is approached.

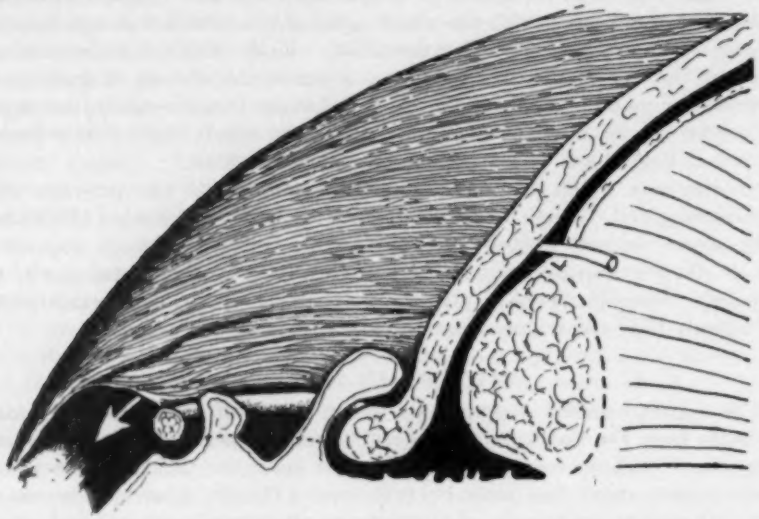

Fig. 1—Elephant oro-pharyngeal isthmus in sagittal section (semi-diagrammatic), showing the mutual relationships of retrolingual gland, velum palatini, epiglottis, arytenoid and naso-pharyngeal sphincter. The arrow occupies the lateral food channel.

The short, narrow, blunt-ended radix linguae is fully accessible only after division of the velum palatini and the reflection of the faucial pillars: this done, and the tongue protracted, the retrolingual glands become obtrusively apparent.

Each is an ovoid, sulcated, mammillated, multiperforate, submucosal sessile mass, tending to lobulation, and forming the convex postero-lateral extremity of the radix linguae. The lobulation is due to the roughly linear arrangement of adjacent component glandular follicles, the mammillation to the lymphoid tissue (lingual tonsil) interposing between the gland acini and the mucosa and the surface perforations are the mouths of the very numerous gland ducts. In the younger elephant specimen examined each mass is approximately 3 cm. long, 2 cm. broad and 2·5 cm. high (and almost contiguous medially with its fellow): in the older specimen each lympho-glandular mass is 3 cm. long, 2·5 cm. broad and 1·5 cm. high (Figs. 2, 3).

HISTOLOGICAL OBSERVATIONS

A pharyngeal gland from the fauces proves to be a highly vascular acinous structure provided with many ducts which proceed directly to the mucosal surface. Predominantly mucous in type, its serous cells are remarkably

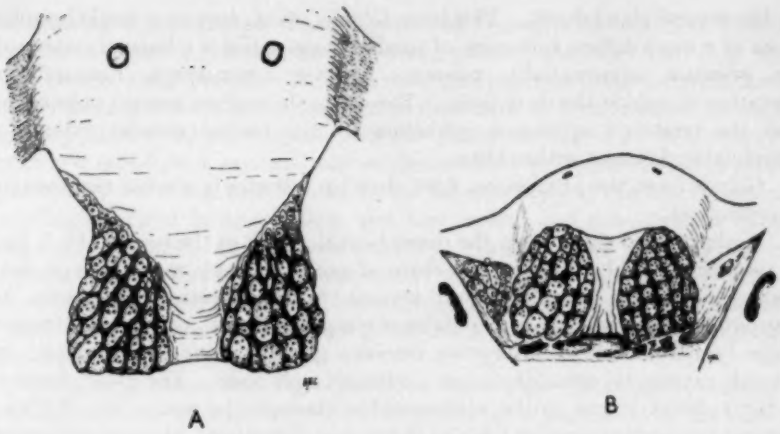

Fig. 2—*Elephas maximus*, ♀ two years (R.232). Showing (A) the dorsal (B) the posterior aspect of the radix linguae and the retrolingual glands.

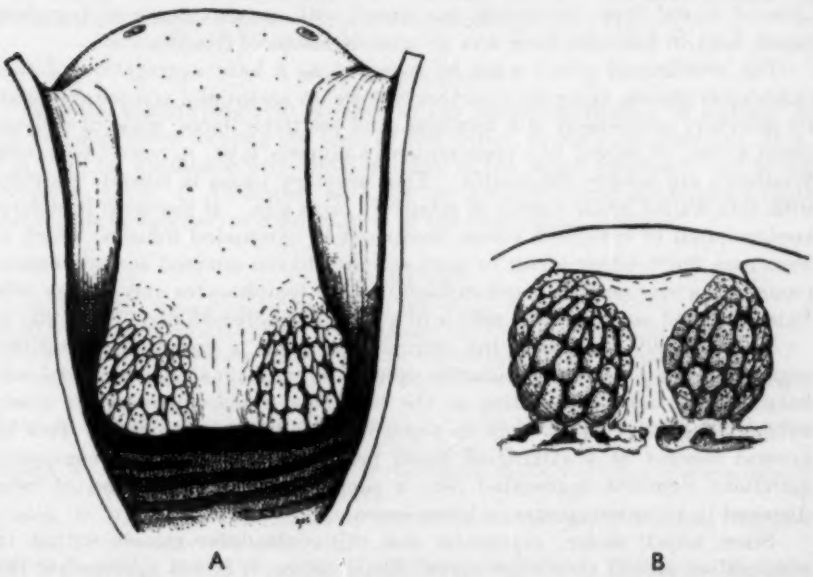

Fig. 3—*Elephas maximus*, ♂ circa nine years (R.228). Showing (A) the dorsal (B) the posterior aspect of the radix linguae and the retrolingual glands.

scanty, though demilunes of Giannuzzi are determinable whenever the preservation is good. Both within the gland itself and alongside its ducts lymphocytes are present in abundance. A large and extremely vascular lymphoid follicle interposes between the gland mass and the mucosa and is tunnelled or skirted

by the several gland ducts. This large follicle, which may be a single lymphoid mass or a more diffuse collection of smaller masses, is not a haemolymph node. Its presence submucosally accounts for the macroscopic mammilliform elevation alongside the duct ostia. The ducts themselves remain independent and the stratified squamous epithelium of the faucial mucosa extends an appreciable distance within them.

Glands from the pharyngeal floor show an essentially similar microscopical constitution.

A pharyngeal gland from the dorso-lateral aspect of the tongue (Pl. I, fig. 1) is likewise a highly vascular structure of predominantly mucous type, manifesting Giannuzzi demilunes and several ducts associated intimately with surrounding lymphocytes and nodules of lymphoid tissue. Again an obtrusively large lymphoid follicle interposes between gland and mucosal surface, and, though extremely vascular, is not a haemolymph node. The gland ducts run a fairly direct course to the surface either through the single large follicle or between secondary smaller follicles in the same situation: they are surrounded by clusters of lymphocytes, which are generally more pronounced as the mucosal surface is approached.

These discrete pharyngeal glands therefore are individual, minor salivary units of mixed type, intimately associated with an abundance of lymphoid tissue, both in follicular form and as concentrations of lymphocytes.

The retrolingual gland must be regarded as a local aggregation of such pharyngeal glands, since its structure follows an essentially comparable plan. Its secretory component is a localised, and relatively large, mass of salivary gland tissue, of mixed but predominantly mucous type, in which Giannuzzi demilunes are readily discernible. This secretory tissue is lavishly provided with thin-walled blood vessels of relatively large size. It lies deep to a dense accumulation of lymphoid tissue, composed of agminated follicles, which its numerous ducts either pierce or skirt *en route* to the mucosal surface, accompanied by a surrounding concentration of both lymphocytes and plasma cells. This lymphoid mass is in the nature of a large haemolymph node (Pl. I, fig. 2).

Histologically, therefore, the retrolingual gland is essentially a salivary organ, of mixed but predominantly mucous type, intimately associated with haemolymph tissue and acting as the functional replacement of the absent sublingual gland. Apart from its topographical location, it departs from the general concept of a sublingual gland principally in having its component glandular elements aggregated into a conglomerate mass instead of being disposed in an antero-posterior linear series.

Since labial, molar, zygomatic and other glandular masses within the mammalian mouth cavity are given official notice, it is but appropriate that the elephant retrolingual gland should likewise be accorded anatomical and nomenclatorial recognition.

FUNCTIONAL CONSIDERATIONS

The functional significance of the elephant retrolingual gland (and of the large and numerous solitary glands of the oro-pharyngeal mucosa) is readily appreciable from a consideration of the nature and quantity of the animal's diet.

This entirely vegetarian pabulum, ingested in considerable amounts, includes both soft material (e.g. fruits, leaves, shoots, grasses, etc.) and hard (e.g. bark, twigs, thorns, small branches). Each mouthful requires to be softened during a fairly rapid mastication and its passage thereafter to be lubricated through a relatively narrow oro-pharyngeal isthmus. To these ends, a copious supply of mucus and moisture is essential and evidence of the presence thereof is plainly witnessed by the abundance of froth in the mouth cavity of the feeding animal. A sublingual gland being wanting, and the parotid and submaxillary glands being relatively small, the requisite quantity of moisture and mucus is perforce supplied by a multiplicity and elaboration of auxiliary (pharyngeal) glands. The retrolingual gland therefore is but a localised aggregation and specialisation of such mucus-producing structures, otherwise distributed fairly uniformly throughout the buccopharynx.

During mastication and deglutition the bucco-linguo-pharyngeal mucosa is inevitably and continuously exposed to some danger of laceration by the harder, abrasive content of the pabulum, and hence to the risk of at least minor infection. The striking abundance of lymphoid tissue and of lymphocytes disposed in the most intimate association with the acini and ducts of the retrolingual and pharyngeal glands would appear to represent an expected defence mechanism against such possible infection.

ACKNOWLEDGMENTS

Grateful acknowledgment is made to the Zoological Society of London for the two specimens forming the basis of this notice, to Mr P. A. Freeman, M.B., F.R.C.S., for assistance with the dissection of the larger specimen, and to my colleague, Dr F. J. Aumonier, both for the accompanying photomicrographs and for his authoritative confirmation of the histological findings.

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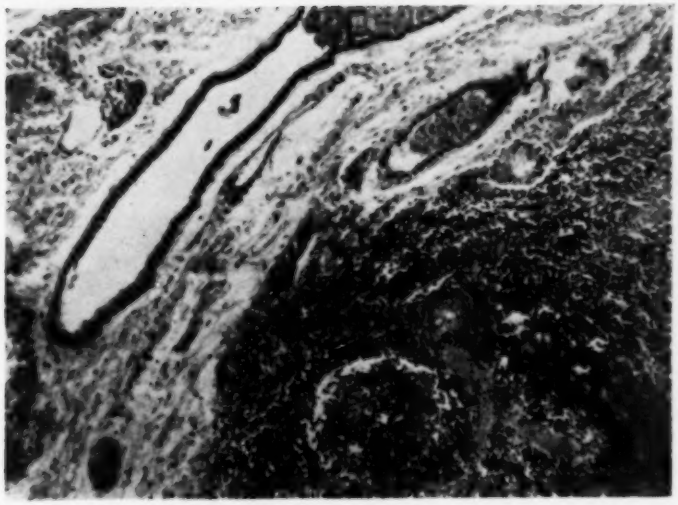

Fig. 1.—*Elephas maximus*. Pharyngeal gland. Stained hæmatoxylin and eosin: × 13. Showing submucosal lymph nodule in relation to two gland ducts.

Fig. 2.—*Elephas maximus*. Retrolingual gland. Stained hæmatoxylin and eosin: × 10. Showing lingual mucosa, submucosal hæmolymph tissue, glandular tissue and gland duct.

NOTICE

["Proceedings", Vol. 136, Part 1, was published on 16th January, 1961.]

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C.4.

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